HABITAT-FORMING INTERTIDAL ALGAE ACROSS WAVE-EXPOSURES: AN EXPERIMENTAL EVALUATION OF PLANT AND HERBIVORE INTERACTIONS

A thesis submitted in partial fulfilment
of the requirements for the Degree of
Doctor of Philosophy
at the
University of Canterbury
New Zealand

By

David Ian Taylor

UNIVERSITY OF CANTERBURY
2002

Abstract

Ecological factors influencing the distribution, survival and growth across wave exposures of different life stages of some intertidal habitat-forming fucoid algae in southern New Zealand and Oregon were examined.

Transect and quadrat sampling in southern New Zealand showed changes in patterns of habitat-forming intertidal algae across wave-exposures. Biomass and species richness across exposures varied greatly and was concentrated in the lower tidal zone. On wave-exposed platforms lower tidal zone biomass was often dominated by the bull kelp *Durvillaea antarctica*, mussels *Perna canaliculus* or suites of red algae (*Gigartina* species). Biomass in the lower tidal zones at moderately exposed platforms was dominated by perennial brown algae like *Cystophora torulosa, C. scalaris* and was dominated by the fucoid alga *Hormosira banksii* and the blue mussel *Mytilus galloprovincialis* at sheltered sites. Invertebrate herbivore abundance and biomass were similar across exposures but the greatest species richness was found in the upper tidal zones. Predator abundance was greatest at sheltered and exposed sites that were dominated by filter-feeder habitats.

Settlement experiments compared the relative ability of *Hormosira banksii*, *Cystophora torulosa* and *Durvillaea antarctica*, to remain attached when exposed to a low energy wave after post-settlement attachment times of 1, 6 and 12 hours. Results showed the exposed shore species *D. antarctica* had better attachment capabilities than *C. torulosa* and *H. banksii* which are more abundant at wave protected sites. In another set of experiments zygotes were subjected to a full 12-hr tidal-cycle in the field after post-settlement attachment times of 1, 6, and 12 hours. *H. banksii* survival was again dependent on post-settlement attachment time and showed a negative relationship with wave exposure while *D. antarctica* survival was not affected by wave exposure or post-settlement attachment time. In identical experiments in Oregon, survival across exposures of *Fucus gardneri* and *Pelvetiopsis limitata* was not significantly different and was largely dependent on sites within exposures. However, a post-settlement time of at least six hours was required for greatest survival of *P. limitata* and *F. gardneri*. These results suggest that sheltered shore species may be constrained in their distribution and abundance across exposures from the outset due to required attachment times.

Transplant experiments using early life stages of habitat-forming large brown algae were done across wave exposures at different times and at different spatial scales in different hemispheres. Specific hypotheses of models of community structure relating to

the effects of grazers across exposures were tested using *Durvillaea antarctica* and *Hormosira banksii* in New Zealand, and *Fucus gardneri* and *Pelvetiopsis limitata* in Oregon. Invertebrate grazer effects were similar across exposures but interactions with ephemeral algae, which were most abundant at exposed sites, and sedimentation at sheltered and intermediate sites were important in both hemispheres. Experiments showed that all species were able to reach the visible recruit stage at all exposures if protected from invertebrate grazers. For all species growth was greatest during spring and summer at wave-exposed sites.

Factors affecting the fine scale distribution of *Durvillaea antarctica* were tested in a canopy removal and substratum clearance experiment repeated at different times over a year. The results showed that the time of clearance affected recruitment of *D. antarctica.* Greatest recruitment was observed under adult canopies at one site and generally recruitment was greatest in coralline removal treatments.

Transplant experiments using *Durvillaea antarctica* recruits were used to test growth and survival across exposures and across coastlines. I found that the distribution of *D. antarctica* across exposures and across coastlines is constrained by the selective grazing activities of the herbivorous fish *Odax pullus.*

Traditional models of intertidal systems often do not reflect changes in the importance of biological and physical factors at different life stages. The innovation of this study is that even over hemispheric scales these intertidal habitat-forming algae are constrained by their life-history characteristics and demographic processes across wave exposures. There were clear differences in the relative abilities of algae to attach quickly to the substratum. At early life stages, the effects of invertebrate grazers were the same across intertidal wave exposure gradients but these affects interacted with growth rates, the environmental effects of sedimentation and the biological interaction with ephemeral algae. For *Durvillaea antarctica*, after reaching the recruit stage its distribution and abundance across exposures and coastlines was determined by the grazing effects of the butterfish *Odax pullus.* I propose a community structure model that incorporates changes in the importance of biological and physical processes at different life stages.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter 3

Chapter 4

Chapter 5

Chapter 6

LIST OF TABLES

Chapter 4

Chapter 5

Chapter 6

ACKNOWLEDGMENTS

Thankyou to everyone who has assisted me during this research project.

First, I would like to thank my supervisor, Associate Professor David Schiel, for his constructive opinions and never-ending ability to see the 'big picture'. I am most appreciative of his guidance in ecological, mathematical and phycological matters.

This thesis would not have been possible without funding from a NIWA / University of Canterbury, Centre of Excellence in Aquaculture and Marine Ecology Scholarship and continued funding from the Andrew Mellon Foundation for which I am extremely grateful.

I want to extend a special thank you to my fellow Ph.D. student, Robyn Dunmore, for being a great colleague, advisor and travelling buddy. Without her guidance and assistance many parts of this project would not have been possible.

During my time at the Edward Percival Field Station in Kaikoura I was assisted in all manner of ways by Jack 'can do it' van Berkel. Thanks Jack for all of your advice and technical expertise. Thanks also to my fellow students and research assistants who helped make my time in Kaikoura interesting and productive, Chris 'you star' Denny, Nathan 'Waka' Walker, Glen 'can you' Thompson, Stacie 'Anne' Lilly, Brent 'the dad' Patrick, Deborah 'the mum' Marshall, Anna 'Rock Girl' Taylor, Nathan 'dive master' Welton, Michael 'gymnast' Anstett , Heidi 'Tara bay' Stevens. Many thanks to my great friends the Hunts, the Bilsburys and Mr. Wilson.

I must also thank Drs. Hickford and Pirker for understanding and encouragement in the face of countless questions about when they were going to finish. I now know what it feels like.

Most recently, I have been helped through advice and encouragement from friends and colleagues, Roly Russell, Matt Bracken, Spencer Wood and the Rilov family.

I want to thank my parents for their undying support and encouragement through the course of my studies. Thanks also to the Gibson family for making me feel part of their family.

Finally, I want to thank my partner, Emma, for having to put up with prolonged periods alone, for standing by me and for her continued love and support.

General Introduction

This thesis examines the relationship between herbivory and wave-exposure on the early life stages of key habitat-forming intertidal brown algae. The underlying philosophy of this thesis is that demographic processes like settlement densities and early – post-settlement survival vary between species across exposures and that their small-scale effects can have larger scale consequences on overall community structure, distribution and abundance.

A study of this type is important for because while wave exposure is often used as a baseline in community structure models the specific wave exposure related processes responsible for determining community structure have rarely been studied experimentally. Much of what is known about the factors determining the distribution and abundance of macroalgae has originated from studies of macroscopic stages and only in the last decade have the roles of propagules and microscopic stages been highlighted (Clayton, 1992; Vadas et al., 1992; Reed, 2000). Macroalgae are the largest primary producers in the exposed intertidal environment in temperate areas (Valiela, 1995) and their importance to the biodiversity and composition of intertidal assemblages is increasingly evident. Their biomass dominates many rocky intertidal shores (Batzli, 1969; Santelices et al., 1980; McQuaid and Branch, 1984), providing food and habitat for numerous invertebrate and fish species (Lubchenco, 1978; Choat and Schiel, 1982; Andrew, 1993). Human populations rely on intertidal algae as a source of food and income in several countries. For example, Chile exports around 40,000 tonnes of dried seaweed products per year (Santelices, 1996).

Despite the biotic and economic importance of intertidal algae many of the processes that determine their patterns of distribution and abundance along shorelines have not yet been examined (Clayton, 1990; Foster, 1990). Historically, intertidal ecologists concentrated their studies on the processes associated with vertical zonation patterns of rocky intertidal species. Vertical zonation patterns of laminarian and fucoid algae, and sessile and mobile invertebrates on rocky shores, are so characteristic they have been the basis of global zonation schemes (Stephenson and Stephenson, 1949; Lewis, 1964; Stephenson and Stephenson, 1972). Many early attempts to understand the processes influencing the vertical patterns of intertidal algae were done by phycologists and concentrated on the relative physiological tolerances of algae to environmental elements associated with tidal emersion. Numerous studies have shown the relative capabilities of

algae to withstand extremes of factors such as, light and temperature (Chapman, 1965; McLachlan, 1974; Lunning and Neushul, 1978), salinity (Hartog den, 1968), tidal ranges and desiccation (Schonbeck and Norton, 1978; Schonbeck and Norton, 1979; Schonbeck and Norton, 1980). Although these factors can all be important, many studies involving physical factors often have the disadvantages of being laboratory-based and of not testing alternative biological alternatives (Schiel, 1981; Underwood and Denley, 1984). In an historical context, an alternative ecological approach has been used by intertidal ecologists in which specific hypotheses about the roles of species' life-history characteristics, demography and behaviour in determining the distributions of intertidal species are tested. These studies have the advantage of being field-based, allowing intertidal species and their interactions with physical and biological factors to be studied and manipulated in their natural environments (Connell, 1974).

Ecological studies over the last thirty years have been particularly successful in elucidating the roles of early life-history factors like settlement and recruitment densities, competitive interactions and selective predation in restricting the distributions of species over intertidal gradients.

Development of experimental ecology

Ecological studies of intertidal communities along intertidal gradients have developed within two convergent philosophical frameworks. Both philosophies have sought to understand the processes determining patterns of species along intertidal gradients but their paths of development have varied (Underwood, 2000). The first philosophy has concentrated on illustrating community-wide dynamics based on the strength of linkages in trophic an d species diversity models and interactions with environmental harshness. The second philosophy has concentrated on specific population demographics and the influences of environmental and biological elements on the recovery, distribution and abundance of species within assemblages.

A major divergence in the two philosophies is often the implied generality of the models they produce. Historically, community models have been promulgated as generally applicable across environments and functional groups (Menge and Branch, 2001). In contrast, models based entirely on population studies apply only to the assemblages studied (Underwood and Denley, 1984). However, a major criticism of many population based studies has been their limited applicability to larger scale questions (Menge and Branch, 2001). One of the major problems faced by marine ecologists is the problem of scale and "how do you test the untestable?". In many cases it is impossible to alter the

nearshore environment at meaningful scales and in meaningful ways to understand the large scale processes acting on intertidal shores. Consequently, marine ecologists are forced to rely on correlations with multiple variables around small scale ecological experiments when approaching large scale topics. Despite these restrictions marine ecology has developed as a model system for many other areas of ecology.

Population demographics

Results of experimentation on populations provide the basis from which community ecology models can be derived. Intertidal systems are particularly amenable to manipulative experimentation because of fast population turnover times and relative ease of access (Connell, 1961a). Early experimental intertidal population studies often concentrated on the relative competitive abilities of species (eg. Connell, 1961a,b), the impacts of predators (eg. Paine, 1966) and the effects of natural disturbances (eg. Dayton, 1971) on their distributions and abundances. Subsequent studies have also shown that variability in arrival numbers, settlement densities, recruitment, growth and reproduction of species can determine the speed of recovery, the outcome of disturbances and amount of competition and predation in intertidal communities (eg. Menge, 1976; Lubchenco, 1978; Sousa, 1979a.b; Connell and Sousa, 1983; Petraitis, 1987; Reed, 1987; Schiel, 1988; Reed, 1990a).

It has been through demographic studies of intertidal populations over the last 30 years that many of the biological and environmental processes determining the distribution and abundance of intertidal populations have been clarified (see reviews by Hoffman, 1987; Schiel 1988; Chapman, 1995; Caley et al., 1996; Underwood, 2000). In recent times larger scale experiments over longer time periods have led to the development of many population-based models (Underwood and Chapman, 1996; Underwood et al., 2000) and to improvements and modifications in several long standing models of intertidal community structure (Menge and Branch, 2001).

Community Structure Models

Early studies of community dynamics in the intertidal zone were greatly influenced by popular terrestrial literature of the time. A key paper by Hairston et al. (1960) introduced a broad-sweeping model regarding trophic interactions determining the distributions and abundances of plants, herbivores and carnivores. They stated that because the accumulation of organic material in most environments is minimal relative to the amount produced by primary producers, food supply must be limiting to species that

decompose matter. Also, the loss of large quantities of plants through natural catastrophic events is anomalous and, therefore, herbivore activity or environmental catastrophes do not limit primary producers. Instead, they must be limited by nutrients. They state, when released of control by carnivores, herbivores deplete primary producers. Therefore, carnivores, rather than plant abundance, limits herbivore populations. Finally, they proposed, for the above to apply, carnivores must be food limited. Many of these predictions have been debated and modified for different environments (eg. Menge and Sutherland, 1976; Van De Koppel, 1996) and have encouraged discussion of the importance of "Top-down" and "Bottom-up" controlling processes to community structure (Carpenter et al., 1985; Menge, 1992; Menge et al., 1997; Menge et al., 1999).

The Hairston et al. (1960) model focused on the links between trophic levels and did not address other areas of community structure. Questions pertaining to the importance of species diversity (Sanders, 1968), the effects of variable recruitment (Underwood and Denley, 1984; Underwood and Fairweather, 1989) and environmental stress (Menge and Sutherland, 1976; Menge and Sutherland, 1987), on community structure and species interactions remained. Paine (1966) and Connell (1978) addressed these questions in their classic papers. Both proposed that diversity is dependent on the interaction between variable predation, competition and the frequency and magnitude of disturbance. They suggested that when competitive exclusion is important at lower trophic levels, species diversity will be greatest at intermediate levels of predation (Paine, 1966), or more generally, disturbance (Connell, 1978). The relationships proposed by Paine's (1966) 'predation hypothesis' and Connells (1978) 'intermediate disturbance hypothesis' have been supported by several field studies (eg. Menge, 1976; Lubchenco, 1978; Sousa, 1979, Hixon and Brostoff, 1983; Kilar and McLachlan, 1989).

To develop these early models and hypotheses further, Menge and Sutherland (1987) produced a synthetic model of species diversity that incorporated the importance of recruitment and environmental disturbance gradients with earlier predictions. Their model predicts that, when recruitment is high, consumers will not be effective at high environmental stress levels, competition for space will not be important and environmental disturbances will be removing species and creating space. In moderately stressful environments mobile consumers will remain unable to control prey abundance and because sessile organisms are assumed to be less affected by environmental stress, they will attain high densities and competition for space will become important. In low stress environments, consumers will be effective at removing prey and prevent competition.

The Menge and Sutherland (1987) model also predicts that at lower recruitment densities the importance of competition will decline but the effects will differ at each trophic level. At higher trophic levels low recruitment is predicted to reduce the importance of competition, even in less stressful environments. At lower trophic levels the importance of competition will decline as recruitment density declines and predation will be the controlling factor in less stressful environments, while disturbance will be the controlling factor in the most stressful environments. Their model also predicts that at high recruitment levels, or if competitive interactions lead to exclusions, the predictions of the 'predation hypothesis' and the 'intermediate-disturbance hypothesis' will not be equivalent and a bimodal function of species diversity will exist along the environmental stress gradient. Harsh environments will have low diversity because only refuge populations and species will survive. As environmental harshness decreases, diversity will increase, because competitive exclusion cannot be fully effective, then decrease as competitive exclusion occurs. It will then increase, as moderate predation prevents competitive exclusion and decrease again, in the least stressful environments, as severe predation causes prey species to become extinct. Finally, they suggest that at low recruitment levels, or if competition fails to exclude species, the predictions of the 'predation hypothesis' and the 'intermediate disturbance model' will be equivalent and the diversity curve will be unimodal.

The complexity of 'environmental stress models' and the vast number of variables encompassed within them have created difficulties in testing many of their predictions and their generality (Menge and Branch, 2001). However, recent modifications, refinements and extensions to include alternative factors like nutrient-related "bottom-up" processes (Menge, 1992; Menge et al., 1997), have seen 'environmental stress models' develop into general tools for comparing systems over large scales (eg. Menge et al., 1999).

Of particular relevance to this thesis are the predictions of the Menge and Sutherland (1987) model regarding variation in the importance of predation (grazing) and competition across gradients of environmental stress. Most models of community structure predict that grazing will be more important in benign environments and grazers will less effective in their control of species and, therefore, competition will be more important under harsh environmental conditions. Results from this thesis will be compared to these predictions.

Environmental and biological elements

As exemplified by environmental stress models, complex interactions of environmental and biological elements act directly and indirectly on communities along intertidal gradients, with both positive and negative effects on their distribution and abundance. The relative influences of these factors depends on the life-stage and physiological characteristics of the species within each community and the demographics of the populations in question (Lotze et al., 2001).

In a review of natural disturbances affecting benthic marine communities, Sousa (2001) lists 20 examples of physical disturbances including waves, logs, ice, sedimentation, lava, water temperature, salinity and lightning strikes. Not surprisingly, many of the environmental disturbances to which intertidal organisms are exposed relate to interactions with the hydrodynamic environment.

Gradients up and along the shore in wave forces, water temperature, salinity, turbidity and oxygen concentration influence the local and regional distribution and abundance of intertidal species (Denny and Wethey, 2001). For intertidal algae, much study has been directed towards understanding the influence of specific hydrodynamic forces on the distribution, morphology and abundance of species. It has been shown that hydrodynamic forces can directly affect fertilization (Pearson and Brawley, 1996; Serrao et al., 1996; Pearson et al., 1998; Serrao et al., 1999a,b), the arrival of propagules (Anderson and North, 1966; Dayton, 1973; Deysher and Norton, 1982; Reed et al., 1988; Santelices, 1990; Kendrick and Walker, 1991; Norton, 1992; Reed et al., 1992; Reed et al., 2000), settlement density (Connell, 1985; Reed, 1990; Fletcher and Callow, 1992; Vadas et al., 1992; Osman and Whitlatch, 1995; Walters and Wethey, 1996), nutrient supply (Amsler and Neushul, 1989; Hurd et al., 1993; Hurd et al., 1996; Creed et al., 1997; Lotze et al., 2001), detachment probabilities and growth form (Vogel, 1984; Koehl and Alberte, 1988; Denny et al., 1989; Gaylord et al., 1994; Denny, 1995; Friedland and Denny, 1995; Hawes and Smith, 1995; Hurd, 2000). Hydrodynamic forces also affect patterns of algae on the shore indirectly, through interactions with waterborne objects, consumers, and by influencing competitive abilities (Sousa, 1979a,b; Lubchenco, 1983; Paine and Levin, 1981; Petraitis, 1990; Dayton et al., 1992; Menge, 1995; Kim, 1997; Underwood, 1999).

The concept of "wave exposure" is frequently used by marine ecologists as an all-encompassing term for gradients in hydrodynamic conditions on intertidal shores but the term has seldom been defined and is usually ambiguous. However, it is generally considered to be a combined index of the physical and hydrodynamic regime to which organisms in the near-shore are exposed (Denny, 1995). In early examples, patterns of

species across wave exposures were used to classify the amount of wave action experienced by intertidal areas (e.g. Ballantine, 1961; Dalby et al., 1978). More recently, the specific hydrodynamic forces, encompassed by the term "wave exposure", have been examined experimentally and the specific drag, lift and acceleration forces experienced by intertidal organisms have been measured (e.g. Norton, 1983; Vogel, 1984; Denny, 1985, 1987; Norton, 1991; Gaines and Denny, 1993; Gaylord et al., 1994; Hawes and Smith, 1995; Denny, 1995; Gaylord, 1999; Hurd, 2000). Also encompassed by the term "wave exposure" are numerous physical elements, including changes in aspect, rock-type, rock hardness, slope, temperature, nutrients and the influx of the coastal water mass along shorelines at small and large scales. This large range of variables can lead to difficulties in designing and maintaining orthogonal experiments and, therefore, in testing models in which the term is used. However, if these limitations and variations are realised and controlled for, it seems wave exposure can be a large-scale surrogate for a range of physical factors and a useful means of structuring experiments.

Biological elements are important controlling agents of community structure and have direct and indirect effects on assemblages. Much early literature concentrated on the direct effects of predation, grazing and competitive abilities (e.g. Connell, 1961; Paine, 1966; Paine, 1974; Menge, 1976; Lubchenco, 1978; Lubchenco and Menge, 1978; Underwood, 1978). More recently, other direct and indirect biotic influences have been illustrated including the effects of canopies, through sweeping, shading and pre-emptive exclusion (e.g. Reed and Foster, 1984; Chapman, 1989; Benedetti-Cecchi and Cinelli, 1992; Sjotun et al., 1998; Jenkins et al., 1999; Underwood, 1999) and the significance of life history and demographic characteristics (e.g. Connell, 1985; Foster, 1990; Schiel, 1990; Brawley and Johnson, 1991; Fairweather, 1991; Amsler et al., 1992; Ang and DeWeerde, 1992; Dayton et al., 1992; Fletcher and Callow, 1992; Norton, 1992; Chapman, 1995; Aberg, 1996; Reed, 2000). Despite the large number of studies in these areas, the relative importance of biological interactions to overall community structure is still unclear in many cases. For example, grazing by limpets has been shown to affect the upper limits of algae worldwide. In most cases, however, environmental elements like desiccation have ultimately determined algal abundance (Hay, 1979; Underwood, 1980; Cubit, 1984; Hawkins and Hartnoll, 1985). As a consequence, experiments testing interactions between organisms are becoming more complex as direct and indirect interactions, within and between species, across larger scales are included (eg. Menge, 1995; Underwood, 1999). Not surprisingly, in the majority of studies the individual life history characteristics of

species have been cited as a major determining factor in the outcome of interactions in intertidal communities (Sousa, 2001).

For intertidal algae, the life history characteristics of individual species vary greatly and can have significant effects on the structure of communities (Sousa, 2001). Variation in reproductive effort (Mathieson and Guo, 1992; Aberg, 1996; Pearson and Brawley, 1996; Reed et al., 1997; Serrao et al., 1999a), spore size, shape, and mobility (Amsler and Searles, 1980; Hoffmann and Camus, 1989; Reed et al., 1992; Santos and Duarte, 1996), dispersal (Anderson and North, 1966; Dayton, 1973; Deysher and Norton, 1982; Reed et al., 1988; Santelices, 1990b; Kendrick and Walker, 1991; Norton, 1992; Reed et al., 1992; Reed et al., 2000; Gaylord et al., 2002), arrival mechanisms (Charters et al., 1972; Moss, 1975; Kennelly, 1987; Reed, 1990a; Vadas et al., 1990; Ang(jr), 1991b; Brawley and Johnson, 1991; Fletcher and Callow, 1992; Becker, 1993; Santelices and Aedo, 1999), growth rates (Huang and Boney, 1983; Reed and Foster, 1984; Wright and Reed, 1990; Vadas et al., 1992) and grazing deterrents (Paul et al., 1987; Hay, 1986; Hay et al., 1988; Hay, 1991; Hay et al., 1994; Hay, 1996) influence the outcome of interactions with the environment and other organisms and can ultimately determine community structure.

New Zealand Intertidal Zone

The patterns of intertidal species on New Zealand shores, particularly in the North East of the country, have been described (e.g. Morton and Miller, 1968). High energy shores are common along the coast of New Zealand, particularly on the West coast, where westerly winds from the Tasman sea predominate. Semi-exposed platforms occur in a few locations and sheltered shores can be found in the lee of peninsulas and within larger harbours. Visually there are considerable differences in the structure of intertidal communities among these shore types, particularly in the mixtures of habitat-forming algae and filter-feeding invertebrate assemblages in the lower tidal zones.

Generally, the lower tidal zones of sheltered shores are dominated by large brown fucoid algae like *Hormosira banskii*, *Carpophyllum* species, *Cystophora* species and the green shell mussel *Perna canaliculus*. Semi-exposed shores have a mixture of *Cystophora* species and the brown bull-kelp *Durvillaea antarctica* and are frequently devoid of filter-feeder assemblages. Exposed coastlines are dominated by *Durvillaea antarctica*, several species of red algae of the genus *Gigartina* and the mussel *Perna canaliculus*.

While the distribution of many of these assemblages around New Zealand has been documented (Knox, 1953; Bantham, 1956; Morton and Miller, 1968; Schiel, 1990) many of the processes determining the distribution and abundance of their component

species have yet to be examined experimentally. However, the relative importance of grazers and physical factors in determining the vertical distribution of *Durvillaea antarctica* was tested by Hay (1979b). Hay (1979b) concluded that while grazers initially constrain the vertical distribution of recruits their vertical distribution was ultimately determined by desiccation. Earlier, Paine (1971) found the mussel *Perna canaliculus* could competitively exclude *Durvillaea antarctica* if starfish (*Stichaster australis*) were excluded from the low tidal zone on the upper west coast of the north island.

To date few experimental field studies have been done on early life-stages of New Zealands' intertidal algae. However, several laboratory-based studies of attachment and growth form of *Hormosira banksii* have been done (e.g. Osborn, 1948; Forbes and Hallam, 1978; Forbes and Hallam, 1979; Begum, 1980; Kevekordes and Clayton, 2000)

Across hemispheres: Experiments in Oregon

For comparison to New Zealand fucoid algae, during the period of my study reciprocal experiments were also done using two fucoid species (*Fucus gardneri* and *Pelvetiopsis limitata*) in Oregon. Oregon is at a similar latitude to southern New Zealand and has some comparable patterns of species across wave exposures. For example, the mid tidal heights on wave exposed platforms are generally dominated by mussel assemblages and the lower tidal zones are dominated by kelp and turfing coralline assemblages (Menge and Farrell, 1989). On the coast of Oregon a rich mosaic of algal species coexist particularly at the lower and upper tidal heights. The fucoid alga *Fucus gardneri* is most abundant in the lower and upper tidal zones and is often closely associated with barnacles. *Pelvetiopsis limitata*, an extremely hardy fucoid, is abundant in the upper tidal zone of many intertidal sites and is also associated with barnacles. Reciprocal experiments were done in Oregon and in New Zealand to compare the influence of life history characteristics, zygote stickablity, grazing and wave exposure on the survival and growth of these habitat-forming species.

A major goal of this thesis is to test predictions of intertidal community models regarding the effects of grazers and the influence of life-history characteristics of habitat-forming algal species across wave exposures using experimental manipulations at local and regional scales to test assumptions and predictions of community ecology models.

This thesis is divided into six sections, which consist of this General Introduction, Chapters 2, 3, 4 and 5 and a General Discussion.

Chapter 2 contains the results of quantitative sampling of biomass, species richness and habitat associations across gradients of wave exposure in southern New

Zealand, in which key organisms and their patterns of distribution and abundance are identified. Included in this chapter are the dynamometer data for main study sites. This provides a context for hypotheses posed in the following chapters.

Chapter 3 presents sets of experiments, testing the relative abilities of early life-stages of habitat-forming algae to remain attached to substratum when exposed to wave forces after different post-settlement attachment times. Experiments were done in New Zealand and Oregon.

Chapter 4 includes experiments testing the effects of grazing and wave exposure on the survival and growth of transplanted early life-stages of habitat-forming algae in New Zealand and Oregon.

Chapter 5 contains the results of experiments on the influences of biological and physical factors on the survival and growth of recruit stages of algae across exposures. The first part deals with the results of an experiment testing the importance of coralline algae and canopy on *Durvillaea antarctica* recruitment, while the second part examines the effects of wave exposure, grazing and canopies on transplanted recruit stages of *Durvillaea antarctica*.

More specific introductions and detailed methodologies are provided at the beginning of each chapter.

1.2. Study Species

Hormosira banksii (Turner) Descaisne

The ubiquitous perennial brown alga *Hormosira banksii* is a dioecious fucoid. It is found on intertidal shores around New Zealand and Southern Australia. It has motile sperm and an egg size of 55-60 μm and, no alteration of generations (Clayton, 1992). It has unique flotation structures that contain seawater and is highly resistant to desiccation (Chapman, 1965; Brown, 1987). It is polymorphic, growing in various forms across a wide range of intertidal habitats, growing up to 40 cm in length (Osborn, 1948; Bergquist, 1959). It is reproductive throughout the year but has pulses in spring and summer. It dominates large areas of the lower and mid tidal-zones on sheltered to semi-exposed intertidal platforms and is found in tide pools and cracks on exposed platforms.

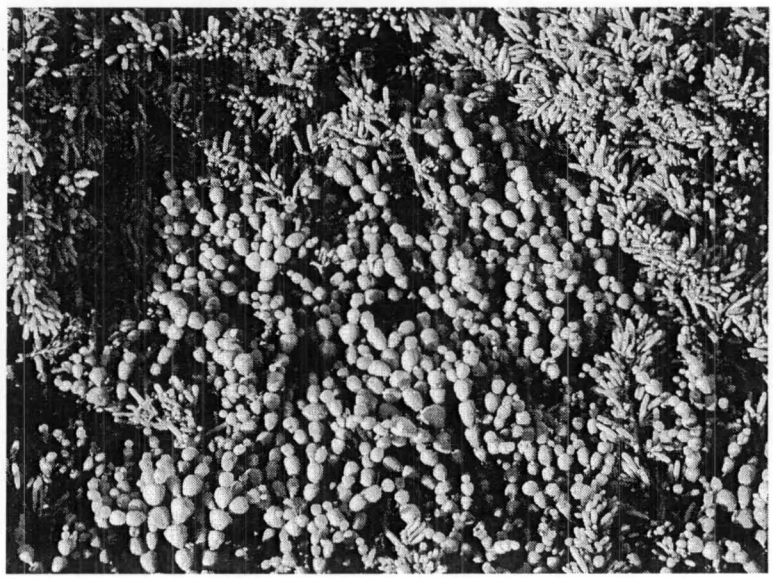

Figure 1.1 *Hormosira banksii* (Centre) and *Cystophora torulosa* (Periphery).

Cystophora torulosa (R. Brown) J. Agardh

The perennial brown alga *Cystophora torulosa* (Family Cystoseiraceae) is one of three species of the genus *Cystophora* (also *C. scalaris, C. retroflexa*) that inhabit the lower intertidal and immediate sub-tidal zone of sheltered and semi-exposed platforms in southern New Zealand. It is a monoecious fucoid that reproduces during spring. It has relatively large eggs (80-100 μm) and it grows up to 1.5m in length.

Durvillaea antarctica (Chamisso) Hariot

Durvillaea antarctica (Family Durvillaeales), is one of the largest fucoid algae in the southern hemisphere, growing up to 10m in length and weighing up to 80 kg. It is dioecious, producing large quantities of small eggs (25-40 μm) in packets of four and sperm in packets of 128 within a sticky mucilage. It is found in the lower tidal zone of semi-exposed to very exposed open coastal reefs in southern Chile and New Zealand and Sub-Antarctic islands. It is polymorphic across habitats (Hay, 1979a). In New Zealand it is regularly found above the other *Durvillaea* species *D. willana* that is strictly subtidal.

Figure 1.2. *Durvillaea antarctica* in the lower tidal zone.

Fucus gardneri Silva

Fucus gardneri is a common perennial intertidal brown alga of the order Fucales which occurs at sheltered to semi-exposed sites in the mid and upper tidal zones from Alaska to Point Conception, CA (Abbott and Hollenberg, 1976). Its thalli grow from a discoid holdfast to 10-25 cm with dichotomous branching. It is monoecious and produces 8 eggs in each oogonia packet with antheridia producing 64-128 sperm. Reproductive receptacles can be found throughout the year, but reproduction peaks during fall and winter (Ang, 1991b). It is also polymorphic and has also been identified as *Fucus distichus* spp. *edentatus* depending on the type locality. It provides habitat for several invertebrate grazer species including the trochid snail *Tegula funebralis, Littorina scutulata* and several species of limpets (*Lottia* species).

Photo by: Gary Allison

Figure 1.3. Picture of *Fucus gardneri* .

1.3. Field Sites

Table 1.1 Description of sites used in experiments (* indicates sites in Oregon).

Site	*Exposure*	*Aspect*	*Rock-type*	*Low-shore*	*Mid-shore*
Island Point	Sheltered	NW	Mudstone	*Perna canaliculus*	*Mytilus sp.*
Jimmy's Beach	Sheltered	NE	Mudstone	*Cystophora species*	*Hormosira banksii*
Devauchelles	Sheltered	NE	Basalt	*Perna canaliculus*	*Mytilus sp.*
Lab Rocks	Sheltered / Intermediate	NE	Mudstone	*Cystophora species*	*Hormosira banksii*
Caves Bay	Intermediate	NW	Basalt	*Carpophyllum maschalocarpum*	*Hormosira banksii*
Moeraki	Intermediate	NE	Mudstone	*C.torulosa* / *D.antarctica*	*Hormosira banksii*
Wairepo	Intermediate	NE	Mudstone	*Cystophora species*	*Hormosira banksii*
Carpark	Intermediate	NE	Mudstone	*Cystophora species*	*Hormosira banksii*
Sharks Tooth	Exposed	E	Mudstone	*Durvillaea antarctica*	*Mytilus sp.*
First Bay	Exposed	E	Mudstone	*Durvillaea antarctica*	*Cellana sp.* / *H. banksii*
Seal Reef	Exposed	E	Mudstone	*Durvillaea antarctica*	*Cellana sp.*
Boulder Bay	Exposed	NE	Basalt	*D. antarctica*	*Mytilus sp.*
Twelve-mile Beach	Very Exposed	NW	Mudstone	*Gigartina* species	*Mytilus sp.*
Thirteen-mile Beach	Very Exposed	NW	Mudstone	*Perna canaliculus*	*Mytilus sp.*
Fogarty Creek*	Very Exposed	NW	Basalt	*Laminaria* sp.	*Mytilus sp.*
Depoe Bay*	Very Exposed	NW	Basalt	*Mazzaella* sp.	*Mytilus sp.*

1.3.1. NEW ZEALAND

Kaikoura Peninsula

Located at 42° 25' S, 173° 44' E on the north-eastern coast of the south island of New Zealand, 200 km north of Christchurch (Fig. 1.5A,B). It has extensive platforms of several rock types including Mudstone, Limestone, Greywacke (Raramai/ Second Tunnel) and projects approximately 4 km out to sea. It has a number of unique features in that it is exposed to a relatively small tidal range and is only a short distance from the continental shelf. It lies close to the Hikurangi trough and is exposed to pulses of upwelling of cold water masses throughout the year with sea-surface temperature ranging from 9 - 18 °C (Chiswell and Schiel, 2001). It lies near the northern end of Southland current that flows up the east coast of New Zealand and is one of the last rocky promontories before the current heads offshore. Rivers to the south of Kaikoura peninsula influence the turbidity and sediment load in the surrounding waters. The majority of the platforms around the peninsula are algal dominated. However, on hard rock (Greywacke) outcrops to the south and north mussels (*Mytilus galloprovincialis, Perna canaliculus*) and barnacles (*Chaemosipho brunnea, Epopella plicata*) are common.

Banks Peninsula

Located at 42° 25' S, 172° 45' E on the central east coast of southern New Zealand (Fig. 1.5A,C). It is composed of mainly volcanic basaltic rock. Sites used in this study were at on the NE side near Godley Head and on the south east side at Devauchelles point in Akaroa Harbour. Banks Peninsula is surrounded by relatively shallow waters and sedimentation and turbidity are influenced by large braided river systems to the north and south. The platforms around the peninsula are characterised by filter-feeder assemblages in the high and mid-tidal levels (mussels *Mytilus galloprovincialis* and barnacles *Chaemosipho brunnea, Epopella plicata*) are common and mixture of mussels (*Perna canaliculus*) large brown algae (*Durvillaea antarctica, Carpohpyllum maschalocarpum*) in the lower tidal levels.

Moeraki Peninsula

Located at 45°11' S, 170°98' E, 520km south west of Kaikoura (Fig 1.5A). It has a range of sedimentary platforms from mudstone to sandstone. The platform used in this study is relatively flat and projects approximately 70m from the shore it is protected by offshore reefs and is rarely subjected to oceanic swells. It is dominated by habitat-forming brown algae in the mid (*Hormosira banksii, Cystophora torulosa*) and lower tidal levels (*Durvillaea antaractica, Xiphophora spp.*). Moeraki peninsula also has large sand beaches to the north and south.

Greymouth

Situated at 42°43' S, 171°21' E on the west coast of southern New Zealand (Fig. 1.5A). Twelve and thirteen mile beach are wave exposed sedimentary platforms that extend out to approximately 150m from the low to the high tidal zone. Both platforms are frequently covered in large quantities of sand and several river systems to the north and south influence sedimentation and along shore nutrient-supply. The platforms are dominated by filter-feeder assemblages in the mid (*Mytilus galloprovincialis*) and upper tidal levels and by a complex of red folliose (*Gigartina* species) and turfing coralline algae in the lower tidal level. The sea-star *Stichaster australis* is abundant in tidal cracks.

Marlborough sounds

Island Point is in Tara Bay in Keneperu sound inside the Marlborough sounds (Fig. 1.5A). It is a sheltered sedimentary platform and was sampled for percent cover, species richness and biomass of habitat-forming species at three shore levels. It was dominated by mussels (*Perna canaliculus, Mytilus galloprovincialis*) and barnacle (*Chaemosipho brunnea*) assemblages at all shore levels.

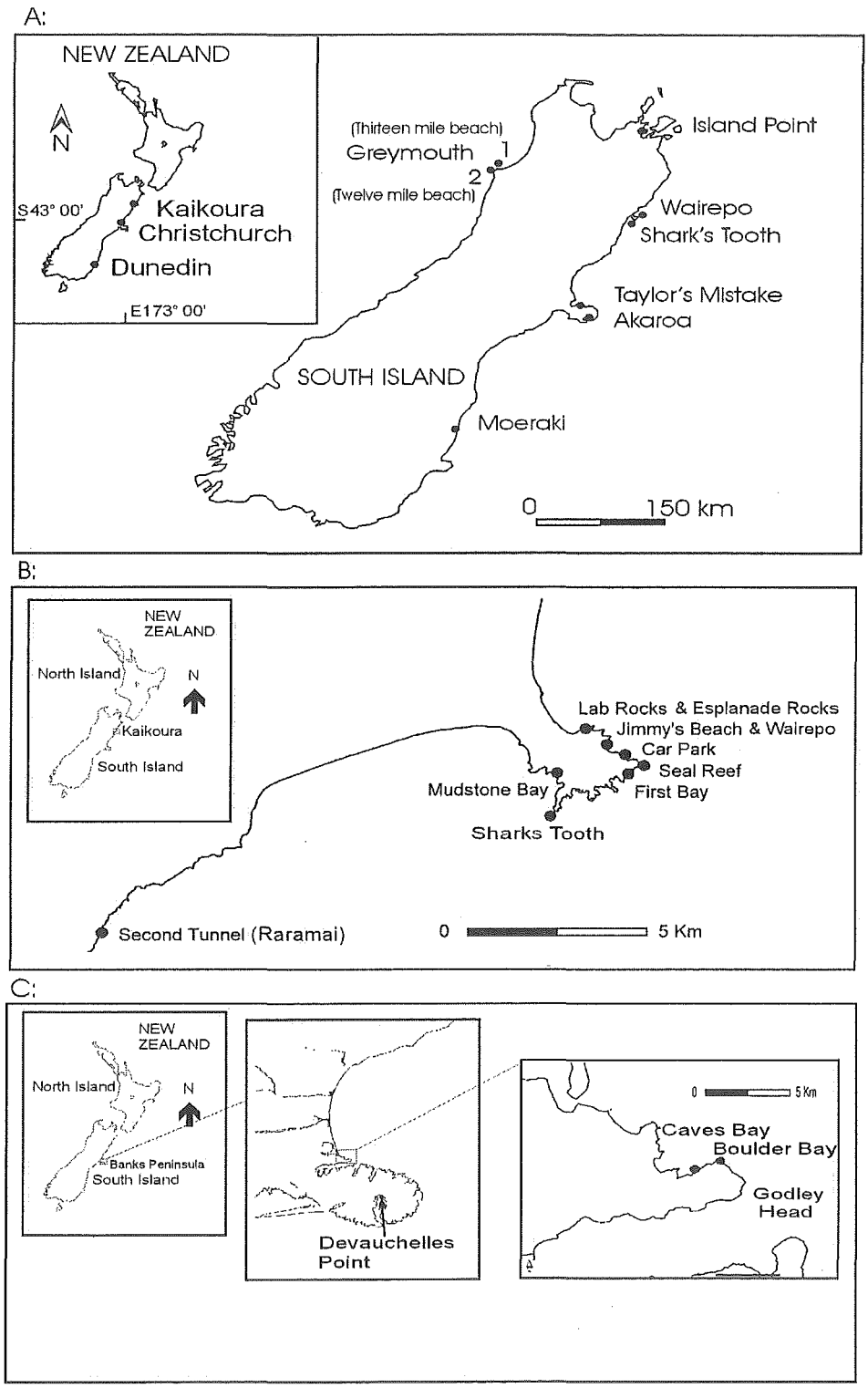

Figure 1.5. Map of : A) the South Island of New Zealand showing the locations of the eight intertidal platforms sampled in chapter 1; B) Kaikoura Peninsula showing the locations of sites used in chapters 2-5; C) Banks Peninsula showing the locations of sites used in chapters 2-4.

1.3.2 OREGON

Fogarty Creek

A basaltic platform located at 44° 51' N,124° 03' W approximately 3.5 km north of Depoe Bay on the Oregon Coast (Fig 1.6). Parts of the platform are exposed to full oceanic swells but semi-protected areas are also present (Blanchette, 1996). The upper tidal levels are dominated by *Fucus gardneri*, *Pelvetiopsis limitata*, *Mastocarpus papillatus*, *Mazzaella cornucopia*, *Endocladia muricata* and the barnacles *Balanus glandula* and *Chthamalus dalli.* Common herbivores in exposed areas are the limpets *Lottia digitalis* and *Lottia strigatella* and the snail *Littorina scutulata.* In more protected areas the trochid *Tegula funebralis* and *Littorina scutulata* are more abundant.

Depoe Bay

A sloping basaltic platform on the central Oregon coast 30km north of Newport (Fig. 1.6). Its southern end is exposed to oceanic swells but the northern end is protected by sandstone platforms to the seaward side. Consequently, a gradient of species can be observed along the platform from the sheltered northern end dominated in the mid and upper tidal levels by *Fucus gardneri*, *Mazzaella cornucopia*, *Neorhodomela larix*, *Odonthalia floccosa*, *Mastocarpus papillatus* and the exposed southern end by the mussel *Mytilus californianus*, barnacles *Balanus glandula* and *Chthamalus dalli* and algae *Pelvetiopsis limitata*, *Mastocarpus papillatus* and *Endocladia muricata*.

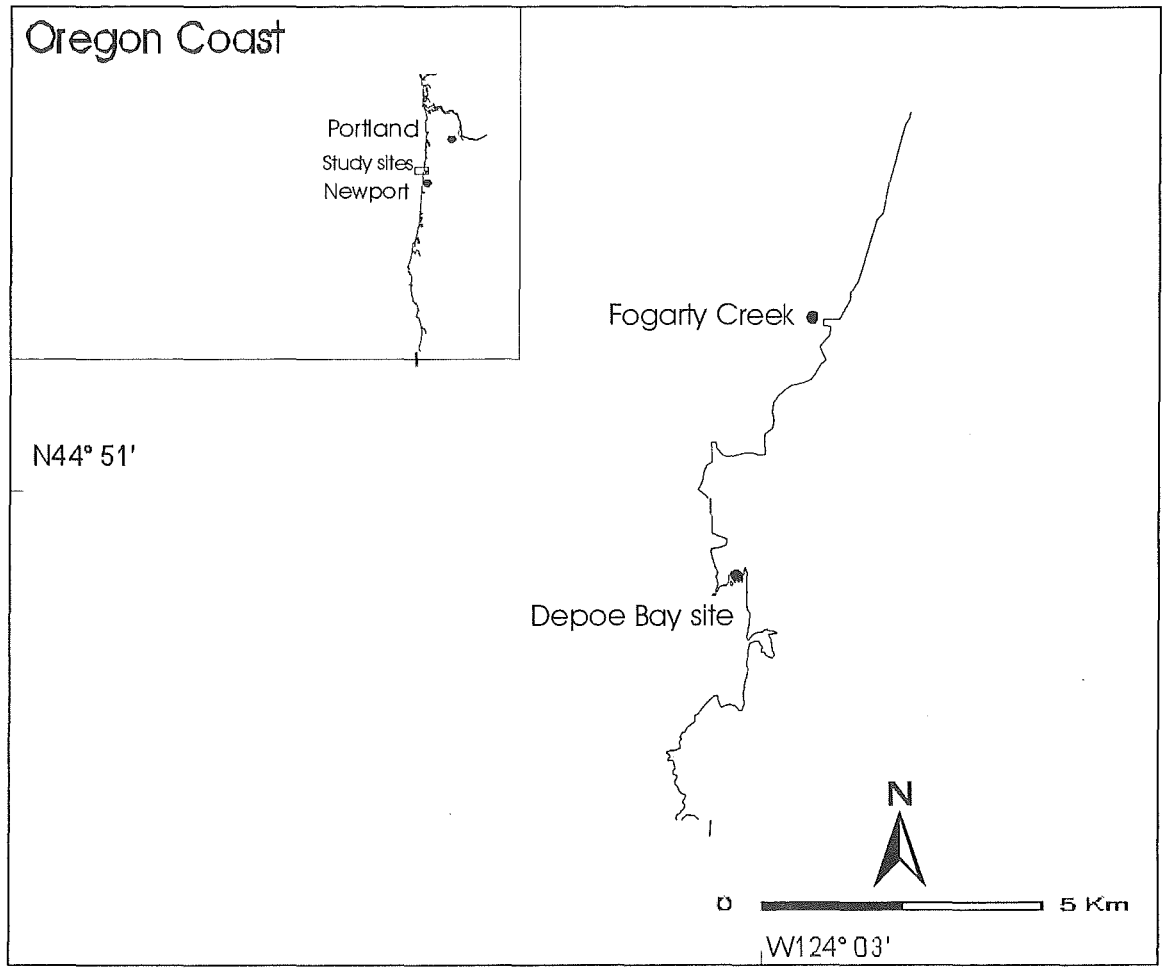

Figure 1.6. Map of Depoe Bay and Fogarty Creek sites on the central Oregon Coast.

Chapter 2

PATTERNS OF ABUNDANCE, BIOMASS AND SPECIES RICHNESS ACROSS WAVE EXPOSURES ON INTERTIDAL ROCKY SHORES OF SOUTHERN NEW ZEALAND

2.1 Introduction

Most models of marine community structure contain some component of exposure. Classical descriptions of intertidal habitats related species' occurrences and zonational patterns to critical tidal heights and a range of physical factors (Stephenson and Stephenson, 1949). More recent models have related the importance of physical factors, competition and predation to different trophic levels within and between communities across environmental gradients, particularly exposure (Menge and Sutherland, 1976, 1987). Other studies have demonstrated that the trophic structure of communities varies significantly with wave action. For example, several studies in southern Africa have shown that filter-feeders and invertebrate predators were more abundant on wave-exposed than on sheltered shores and that semi-exposed and sheltered shores tended to have greater species diversity (McQuaid and Branch, 1984, 1985; Bustamante and Branch, 1996; Bustamante et al., 1997). However, if models involving environmental gradients are to be of general use (c.f., Menge and Olson, 1990), the term "exposure" must be clearly defined and it must be clear whether or not exposure-related patterns apply to other areas of the world.

One complication is that "exposure" can have several meanings and is only one of several potential correlates of the biological structure of shores. Within shores, for example, there is a gradient of physical conditions related to tidal height, particularly temperature, immersion and emersion times and desiccation stress (Connell, 1972,

1975). Among shores, there can be very large differences in wave exposure that potentially affect assemblages and their structuring processes. Although seldom defined, "wave exposure" is generally regarded as a combined index of the harshness of the physical and hydrodynamic environment to which organisms on the nearshore are exposed (Denny, 1995). Variables encompassed by wave exposure can generally be divided into the direct effects of hydrodynamic forces such as drag and acceleration, and the indirect effects of modified physical and biological environments (Vogel, 1984). To lend a more rigorous definition to wave exposure, many studies have used dynomometers and oceanic wave data to give a measure of wave force among shores (Jones and Demetropoulos, 1968; Denny and Gaines, 1990; Bell and Denny, 1994; Denny, 1995; Menge et al., 1999).

Shores of differing exposures tend also to have large differences in several other physical factors such as substrata hardness, shore aspect and steepness, temperature, nutrient regimes (Raffaelli and Hawkins, 1996) and the influx of coastal water masses (Wuff and Field, 1983; Vincent and Howard-Williams, 1991; Menge et al., 1999). Wave exposure, therefore, tends to be used mainly as a large-scale surrogate of a range of physical factors, and may be a useful means of structuring experiments (Connell and Slatyer, 1977; Kautsky and Kautsky 1989; Menge and Olson, 1990; Menge, 1995). Here, we use wave exposure simply as a descriptor of the wave climate experienced by a particular site.

The shores of New Zealand, particularly in the north of the country, have been classified according to their biota and relative exposure (Morton and Miller, 1968). However, there are few quantitative data on the variation within and among shores in diversity patterns, species' abundances and biomass (cf., Paine, 1971). The shores of southern New Zealand have been generally described (Knox, 1953; Batham, 1956; Moore, 1961; Raffaelli, 1979; Marsden, 1985) but not across the full range of physical habitats that exist. High-energy shores are common, particularly on the west coast exposed to the westerly winds of the Tasman Sea and on headlands along the east coast

(c.f., Menge et al., 1999). Semi-exposed platforms occur in a few places on the east coast (Schiel and Taylor, 1999) and sheltered shores occur in the lee of various headlands and within the larger harbours (Batham, 1956; Morton and Miller, 1968). Visually, there is considerable variation in intertidal habitat structure among these various types of shores, particularly in habitat-forming algae and filter-feeders.

In this chapter, I examined effects of wave exposure, location on the island and tidal height on species richness, abundance, biomass in the rocky intertidal on the South Island of New Zealand. I confined my sampling to one month in one year and to a restricted geographic area to limit the influence of the temporal and wider biogeographic patterns that exist over the full length of New Zealand (Moore, 1961; Adams, 1994).

2.2 Materials and methods

Eight study sites were arbitrarily selected from the accessible parts of the east and west coast of the South Island (see Fig. 1.5). Two sites were grouped into each of four "exposure" classes, based on an initial subjective assessment of their relative exposure to waves and storms. These exposure classes were sheltered, semi-protected, exposed and very exposed. Within exposures on the east coast, replicate sites were separated by hundreds of kilometres. The "very exposed" sites occurred only on the west coast, where the sites could not be widely separated because of inaccessibility of many sites. To verify the differing degrees of wave exposure, a site within each exposure class on the east coast was later fitted with five replicate dynomometers (c.f., Bell and Denny, 1994), left in place for three months and sampled monthly to give a relative measure of the wave force.

"Sheltered" sites were at Akaroa (AK) and Island Point (IP). These were in embayments and were protected from oceanic swells. "Semi-protected" sites were at Moeraki (MO) and Wairepo (WA). These were open-coast platforms sheltered by offshore reefs but occasionally subjected to storm-generated waves. "Exposed" sites were at Taylors Mistake (TM) and Sharks Tooth (ST), which were generally exposed to

oceanic swells. "Very exposed" sites were near Greymouth (GM1 and GM2); these were on the high-energy west coast and exposed more or less continuously to large oceanic swells generated by the prevailing westerly winds.

The basis of all tests and descriptions was *in situ* sampling of random quadrats, for estimates of abundance, and complete clearances of all biota for later analysis in the laboratory for the abundance of smaller organisms and biomass estimates of all organisms. Most organisms were identified to the species level, although this was not possible for some of the smaller invertebrates. The main authorities used for taxa identifications were Adams (1994) for algae, Powell (1979) for gastropods, McLay (1995) for polychaetes and amphipods, and Morton and Miller (1968) for many other species. At each site, sampling was done within each of three tidal zones, based on the relative demarcation of major habitats from previous studies (Morton and Miller, 1973; Raffaelli, 1979; Schiel and Taylor, 1999). The low tidal zone was from 0.1 to 0.4m (above Chart Datum) and encompassed the biota on the intertidal-subtidal interface. The mid tidal zone was from 0.5 to 0.8m, and the high tidal zone was from 0.9 to 1.2m above chart datum. Sampling was done in January 1998 during a period when low tides were at the 0.1m mark above Chart Datum (N.Z. Nautical Almanac, 2000). Within each tidal zone at each site, a 50m transect tape was haphazardly placed, ten 0.25m^2 quadrats were randomly selected along the transect and all organisms larger than about 0.2cm across were counted or assessed for percentage cover. Quadrats were divided by strings into 100 squares. The percentage cover of algae and encrusting invertebrates such as barnacles was assessed by estimating the proportion of each square covered by a species. To assess the abundance of smaller species, such as amphipods and small algae, and the biomass of all organisms, three further random quadrats of 0.0625m^2 were completely sampled by using a flat shovel to scrape everything from the rocky surface. These samples were bagged and taken back to the laboratory for sorting, identification of species and drying to a constant weight at 60°C. Biomass values for molluscs are expressed as shell-free dry weights (S.F.D.W) (grams $\pm$ 1 standard error).

Abundance data for many individual species and bare space are graphed. Many coralline algae could not be identified to the species level and were grouped into geniculate and non-geniculate corallines. Other species were identified but then grouped into categories (e.g., mussels and barnacles). Finally, functional groupings (e.g., algae, filter-feeders, predators and grazers) were used to compare the patterns found in our study to those in other studies (e.g., McQuaid and Branch, 1985; Menge and Sutherland, 1987).

The primary statistical analysis was an analysis of variance using (Statistica 5.0 (Statsoft Inc.), with main fixed factors of "exposure" (= 4) and "shore zone" (= 3), and a nested random factor of "sites within exposure" (= 2). Data were tested for homogeneity of variances using Cochran's test prior to analyses and data were transformed when necessary. In all cases, these tests were non-significant unless otherwise stated. In some cases (see Results) the variances could not be stabilized, so results should be cautiously interpreted (c.f., Underwood, 1997).

2.3 Results

One hundred and sixty-four species were encountered and identified in this study across all study sites (Appendix A). Most of these occurred in at least two of the four exposure levels

2.3.1 Wave force

Maximum wave force data from dynamometers confirmed the categorization of the east coast sites into sheltered, semi-protected and exposed (Fig. 2.1). Average wave forces ranged from 2-4 N at the sheltered site, 12 – 35 N at the semi-protected site and 35 – 50 N at the exposed site. Semi-protected sites converged in maximum wave forces during autumn months (March-April).

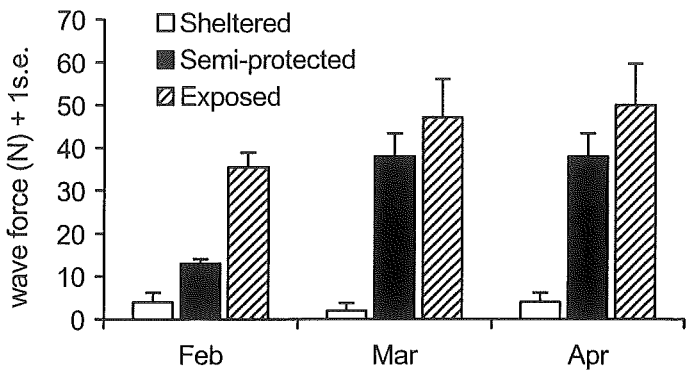

Figure 2.1. The average maximum wave force (Newtons) recorded at three east coast sites (Akaroa, Wairepo and Taylors Mistake) using dynamometers (n= 5 at each site) during Feb. – Apr. 1998.

2.3.2 Percent cover and Abundance

Algae and bare space

Macroalgae dominated more than eighty percent of substratum in the low tidal zone of all the semi-protected, exposed and very exposed sites and the mid tidal zone of the semi-protected sites (Fig. 2.2A). There was dense layering of algae in the low zone at the semi-protected Moeraki site. Virtually no macroalgae occurred in the upper tidal zone at any site. The bull kelp *Durvillaea antarctica* dominated the low zone at Moeraki (semi-protected), Sharks Tooth and Taylor's Mistake but was not found at the very exposed Greymouth sites or at the two sheltered sites (Fig. 2.2B). At Moeraki, *D. antarctica* occurred only on exposed promontories jutting from the reef. Species of the fucalean genus *Cystophora*, in particular *C. torulosa*, dominated the low zone at Wairepo (Fig. 2.2C). Another fucalean, *Hormosira banksii*, dominated the mid-tidal zone at the two semi-protected sites (Fig. 2.2D) and occurred only in small and patchy abundances elsewhere. Many species of foliose red algae occurred at most sites but were dominant only in the low tidal zone of the very exposed sites (Fig. 2.2E). The dominant species at these sites were the very tough *Gigartina* species, particularly *G. decipiens* and *G. clavifera*. The variation in the abundance of macroalgae across

exposures and tidal zones is shown by significant treatment effects (Table 2.1A). Sites within exposures were not significantly different.

Associated with the macroalgal canopy at all sites was a sub-canopy of turfing geniculate (Fig. 2.2F) and encrusting non-geniculate (Fig. 2.2G) coralline algae. The geniculate corallines were particularly abundant beneath the *Hormosira* canopy at the semi-protected sites and the *Gigartina* canopy at the very exposed sites. Both of these algal groups varied significantly between sites within the exposures and across the tidal zones (Table 2.1B, C).

Bare space varied considerably across tidal zones and sites (Table 2.1D). Bare space averaged around 40% of the low and mid tidal zones at both sheltered sites and dominated the upper zone at the sheltered and semi-exposed sites (Fig. 2.2H). The exposed sites had the least bare space over all of the tidal zones.

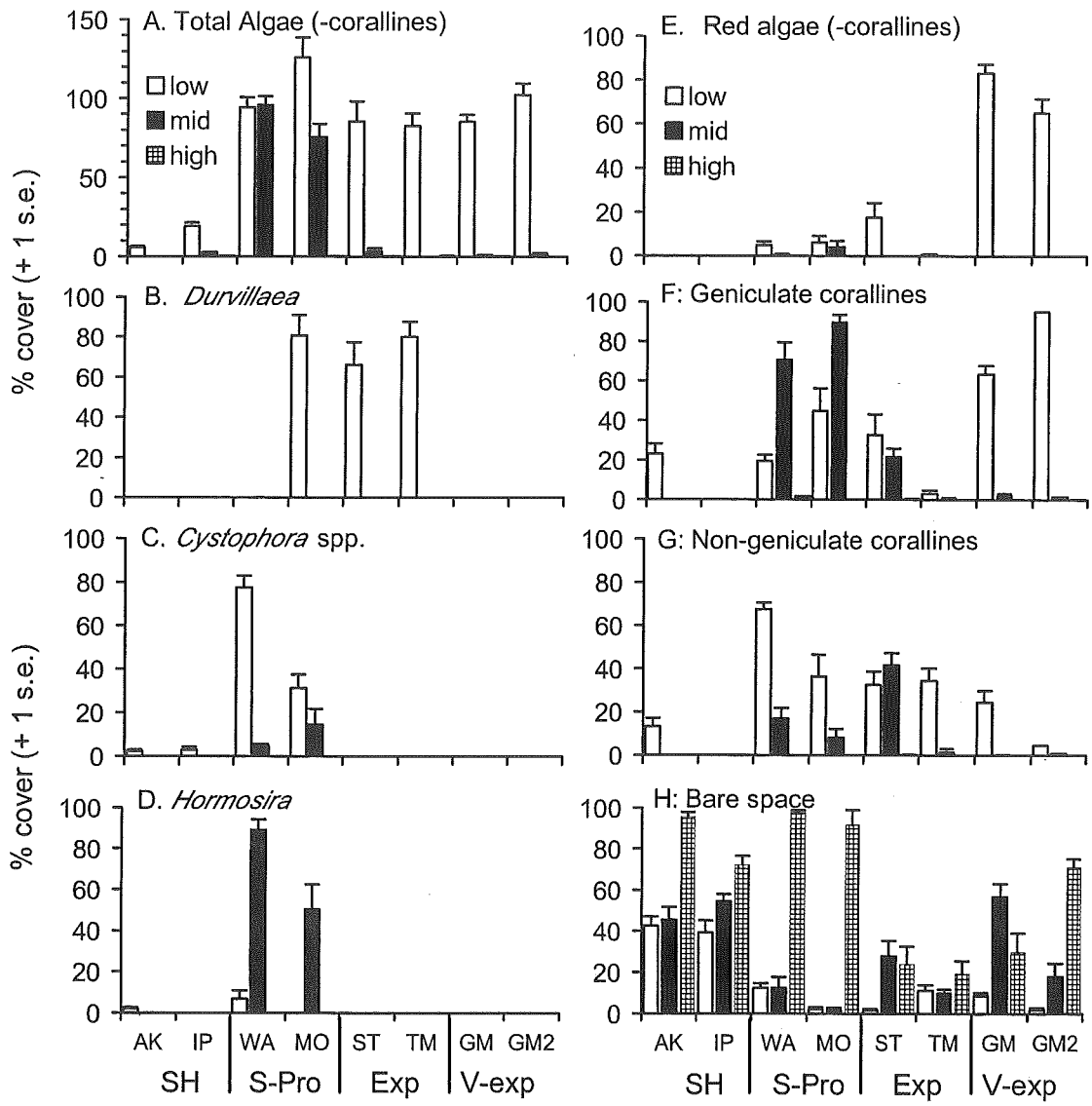

Figure 2.2. The average percentage cover of total macroalgae (- corallines) (A), *Durvillaea antarctica* (B), *Cystophora* spp. (C), *Hormosira banksii* (D), red algae (E), geniculate corallines (F), non-geniculate corallines (G) and bare space (H), in the Low, Mid and High tidal zones of all sites across the four exposure levels (Sheltered, Semi-protected, Exposed, Very-exposed).

Filter-feeder assemblages

Filter-feeders were abundant at all sites and exposures except for at the semi-protected sites (Fig. 2.3A). They varied considerably in abundance between sites within exposures, especially at the exposed sites, and also between the tidal zones at these sites (Table 2.1E). In most cases, the dominant cover was by mussels, particularly *Mytilus galloprovincialis* and *Perna canaliculus*, which had a bi-modal distribution with respect

to exposure. They were abundant in the low and mid tidal zones at protected sites, were very scarce in the semi-protected sites, occurred abundantly in only one of the exposed sites, reaching up to an average of 50% cover, and dominated the cover at the very exposed sites, with up to 90% cover (Fig. 2.3B). Mussels occurred in the mid and upper tidal zones at the very exposed sites, compared to the lower zones at the less exposed sites. At the exposed site of Sharks Tooth there were few mussels or other filter-feeders in the low and mid zones, which were dominated by *Durvillaea antarctica* and coralline algae (Fig. 2.2). Barnacles, particularly *Epopella plicata*, *Chaemosipho columna* and *C. brunnea*, were found at most sites but reached a dominant cover of >60% only in the upper tidal zone of the exposed sites (Fig. 2.3C). In the upper zone of one protected site, *Chaemosipho* spp. reached an average of 20% cover, while a similar cover at the very exposed sites was predominantly *Epopella*. Tubeworms were common only at the sheltered sites, particularly in the lower and mid tidal zones (Fig. 2.3D). For all of these species, there were significant exposure x zone interactions (Table 2.1)

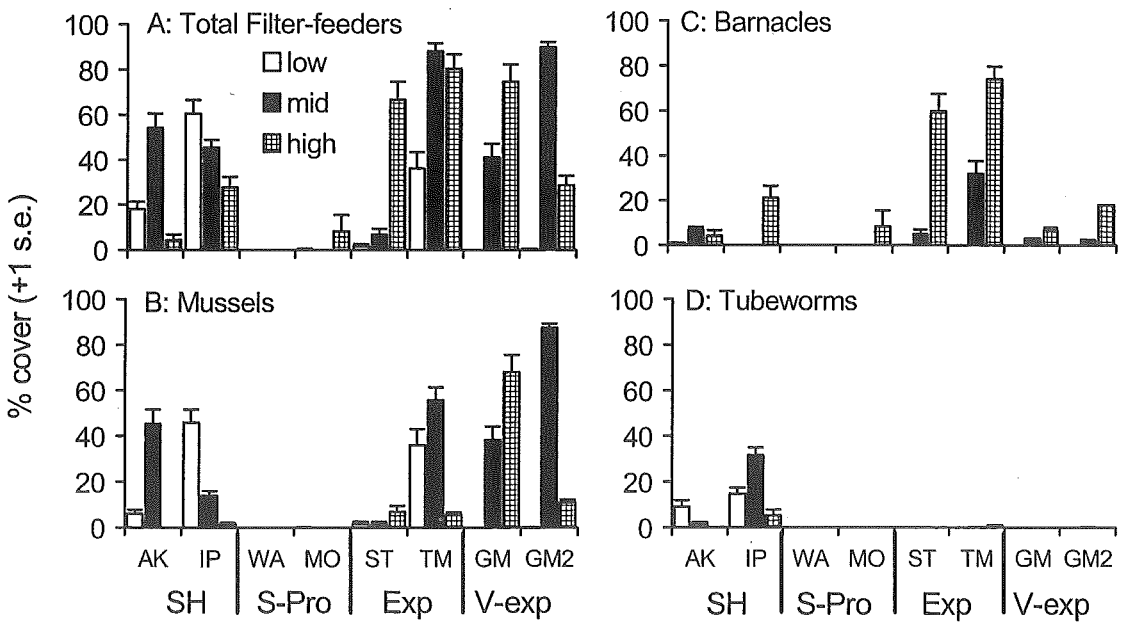

Figure 2.3. The average percentage cover of all filter-feeding species (A), mussel species (B), barnacle species (C) and tubeworm species (D) in the Low, Mid and High zones of all sites across the four exposure levels.

Table 2.1. Three factor analyses of variance of the effects of exposure, sites within exposure and shore zone on the average percentage cover per 0.25m^2 of (A) algae, (B) geniculate corallines, (C) non-geniculate corallines, (D) bare space and (E) filter-feeders. Some data were transformed using [1] $(x)^{0.5}$ to stabilize variances; [2] denotes cases where variances could not be stabilized and cochran's tests were significant.

Group	Source	df	Ms	F	p
A: [2] Algae	Exposure	3	32844.2	113.14	0.000***
	Sites (Exp.)	4	290.3	1.47	0.213
	Shore Zone	2	106908.9	331.70	0.000***
	Exp. x zone	6	18335.7	56.89	0.000***
	Sites (Exp.) x zone	8	322.3	1.63	0.117
	Residual	216	197.63		
B: [2] Geniculate corallines					
	Exposure	3	4587.05	5.86	0.060
	Sites (Exp.)	4	2488.50	15.99	0.000***
	Shore Zone	2	25268.02	21.39	0.001**
	Exp. x zone	6	16703.58	14.14	0.001**
	Sites (Exp.) x zone	8	1181.03	7.59	0.000***
	Residual	216	155.62		
C: [1] Non-geniculate corallines	Exposure	3	106.85	3.55	0.126
	Sites (Exp.)	4	30.07	23.64	0.000***
	Shore Zone	2	371.38	14.4	0.002**
	Exp. x zone	6	30.68	1.19	0.398
	Sites (Exp) x zone	8	25.79	20.27	0.000***
	Residual	216	1.27		
D: [2] Bare	Exposure	3	18169.19	32.98	0.003**
	Sites (Exp.)	4	550.89	2.50	0.043*
	Shore Zone	2	49183.80	18.89	0.000**
	Exp. x zone	6	8293.46	3.19	0.066
	Sites (Exp.) x zone	8	2603.50	11.83	0.000***
	Residual	216	220.07		
E: [2] Filter-feeders	Exposure	3	24283.43	2.79	0.174
	Sites (Exp.)	4	8713.66	51.25	0.000***
	Shore Zone	2	414716.05	12.75	0.123
	Exp. x zone	6	10157.33	1.89	0.197
	Sites (Exp.) x zone	8	5349.08	31.46	0.000***
	Residual	216	170.01		

Grazers

Both large and small molluscan grazer abundance varied considerably between sites within exposures, and also between the tidal zones at these sites (Table 2.2A, B). The larger grazers were the turbinid gastropods *Turbo smaragdus*, the trochid *Melagraphia aethiops*, patellid limpets of the genus *Cellana*, the chiton *Chiton pelliserpentis* and the siphonarid limpet *Siphonaria zelandica*. These larger grazers occurred at all sites and within all tidal zones, reaching overall densities of >50 per 0.25m^2 (Fig. 2.4A). The most abundant smaller molluscan grazers were the littorinids *Littorina unifasciata* and *L. cincta*, the potamidid *Zeacumantus subcarinatus* and the acmaeid limpets *Notoacmea pileopsis* and *N. parviconoidea*. These were very abundant at some sites, reaching densities of hundreds to thousands per m^2 in the upper tidal zones of the exposed sites and at the very exposed Greymouth site (Fig. 2.4B).

Turbo was the largest of the grazing gastropods, with an average shell width of *c.* 24mm. It was greatly abundant on the low shore of one sheltered site (21 per 0.25m^2) but also had average densities of *c.* 5 per 0.25m^2 in the mid tidal zones of the two semi-protected sites (Fig. 2.4C). *Melagraphia*, which feeds mostly on algal films, was found only on the more sheltered sites (Fig. 2.4D). It occurred at all tidal levels in the sheltered sites, where it reached average densities of 14 per 0.25m^2, but was also very abundant in the upper tidal zone at the semi-protected Wairepo site.

Limpets of the genus *Cellana* were found at all sites but tended to be most abundant on the upper shore of the very exposed sites and in the mid tidal zone of one semi-protected site (Fig. 2.4E). There was, however, a difference in how individual species were distributed among sites and exposures. The large *C. denticulata* and *C. flava* (both reaching up to *c.* 75mm in shell length) occurred mostly in the mid tidal zone of the more sheltered sites and were exclusively associated with patches that were either bare or else had a thin cover of encrusting coralline algae. *C. ornata* and *C. radians* (the *perana* form; Powell, 1979) were the dominant limpet species in the upper tidal zone of the more exposed sites. They were particularly abundant in the small bare

spaces among patches of mussels on the mid shore and barnacles on the upper shore in the very exposed sites, where they reached average densities of 50 per 0.25m^2.

Another common limpet was the pulmonate *Siphonaria zelandica* that was found at all exposures, it reached its greatest average densities of 15 per 0.25m^2 in the mid tidal zone at the sheltered Akaroa site (Fig. 2.4F). *Chiton pelliserpentis* occurred mostly in the low and mid zones at all sites, with average densities of 3-5 per 0.25m^2 (Fig. 2.4G). However, it was particularly abundant at the protected Island Point site where it reached average densities of 7 per 0.25m^2.

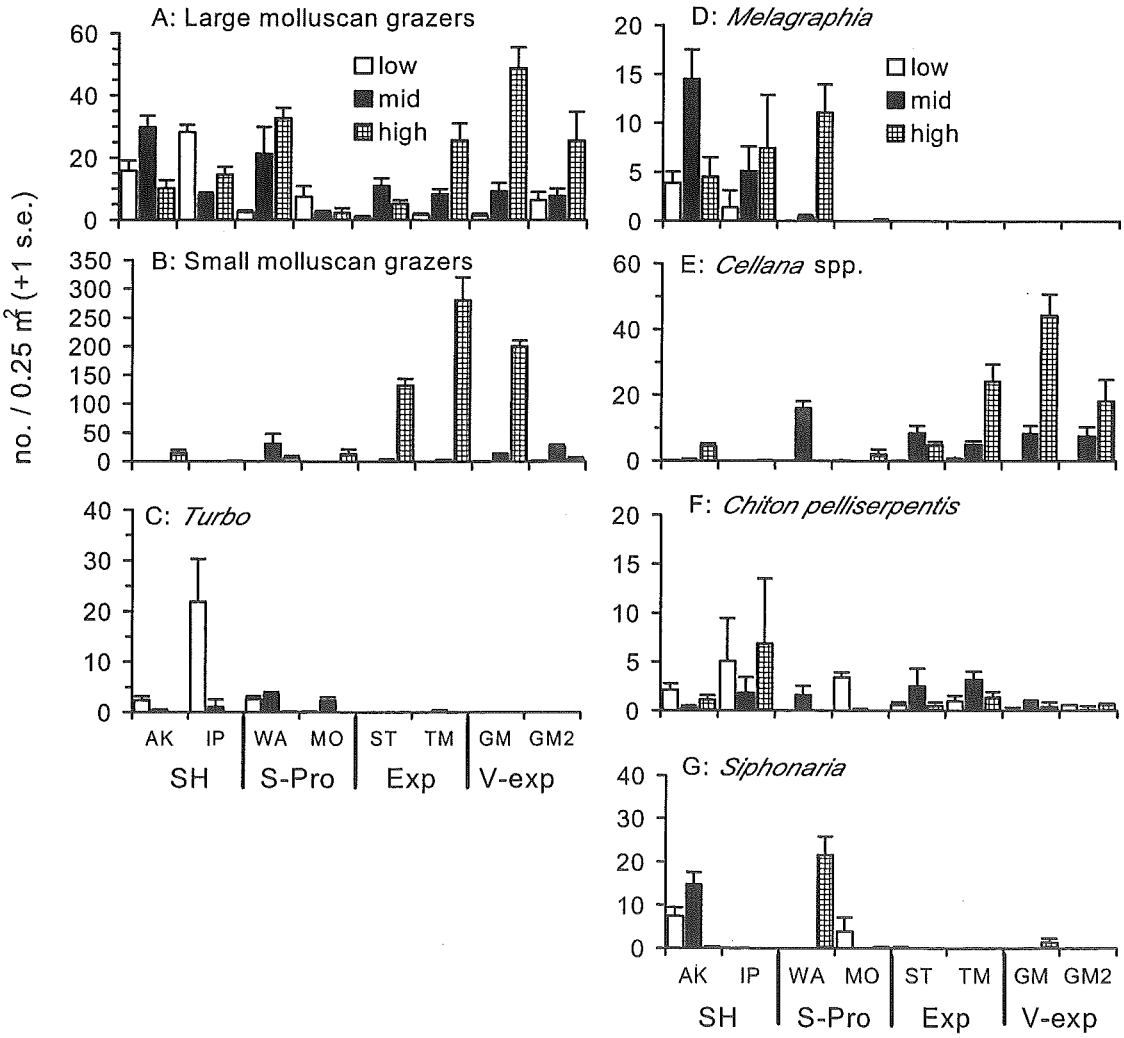

Figure 2.4. The abundance per 0.25m^2 of large molluscan grazers (> 1cm)(A), small molluscan grazers (< 1cm) (B), *Turbo smaragdus* (C), *Melagraphia aethiops* (D), all *Cellana* species (E), *Chiton pelliserpentis* (F) and *Siphonaria zealandica* (G) in the Low, Mid and High tidal zones of all sites across the four exposure levels.

Table 2.2. Three factor analyses of variance of the effects of exposure, sites within exposure and shore zone on the average abundance per 0.25m^2 of (A) large grazers >15 mm, (B) small grazers <15mm and (C) total predators. Some data were transformed using [1] $(x)^{0.5}$ to stabilize variances; [2] denotes cases where variances could not be stabilized and Cochran's tests were significant.

Group	Source	df	Ms	F	p
A: [2] Large grazers	Exposure	3	14170.41	1.31	0.386
	Sites (Exp.)	4	10801.44	37.06	0.000***
	Shore Zone	2	1805.47	0.47	0.643
	Exp. x zone	6	4611.56	1.19	0.398
	Sites (Exp.) x zone	8	3868.33	13.27	0.000***
	Residual	216	291.49		
B: [2] Small grazers	Exposure	3	57233.5	2.50	0.201
	Sites (Exp.)	4	23142.4	28.39	0.000***
	Shore Zone	2	161576.8	6.02	0.025*
	Exp. x zone	6	60015.6	2.24	0.145
	Sites (Exp.) x zone	8	26847.7	32.93	0.000***
	Residual	216	815.25		
C: [1] Total Predators	Exposure	3	29.64	1.00	0.479
	Sites (Exp.)	4	29.60	33.47	0.000***
	Shore Zone	2	7.80	0.55	0.594
	Exp. x zone	6	10.73	0.76	0.618
	Sites (Exp) x zone	8	14.05	15.88	0.000***
	Residual	216	0.88		

Predators

Non-cryptic predators were most abundant in the sheltered and more exposed sites (Fig. 2.5A). They tended to occur where there were the greatest densities of mussels and barnacles. Their abundances varied significantly between sites within exposures, and among tidal zones within sites (Table 2.2C). Seastars were found at five of the eight sites but usually at low densities (Fig. 2.5B). The small pincushion star *Patiriella regularis* reached average densities of 4 per 0.25m^2 on the low shore and 1 per 0.25m^2 on the mid shore of the sheltered Island Point site. The larger (*c.* 200mm across)

Stichaster australis was common in the mid tidal zone of the very exposed sites, where it reached average densities of *c.* 2 per 0.25m^2. The predatory whelk *Haustrum haustorium* was essentially an exposed-coast species. It reached average densities of 1-3 per 0.25m^2 at the exposed Taylors Mistake site and at both very exposed sites (Fig. 2.5C). The whelk *Lepsiella scobina* reached densities of *c.* 5 per 0.25m^2 in the upper tidal zone on one exposed site (Fig. 2.5D), and was observed feeding on barnacles. The whelk *Cominella maculosa* reached densities of 2.5 per 0.25m^2 in the low tidal zone of the sheltered Island Point site and *C. glandiformis* occurred at 1 per 0.25m^2 at the very exposed Greymouth 2 site (Fig. 2.5E). The whelk *Thais orbita* was confined to the exposed Taylors Mistake site and the very exposed sites reaching densities of 1.5 and 0.5 per 0.25m^2 respectively (Fig. 2.5F).

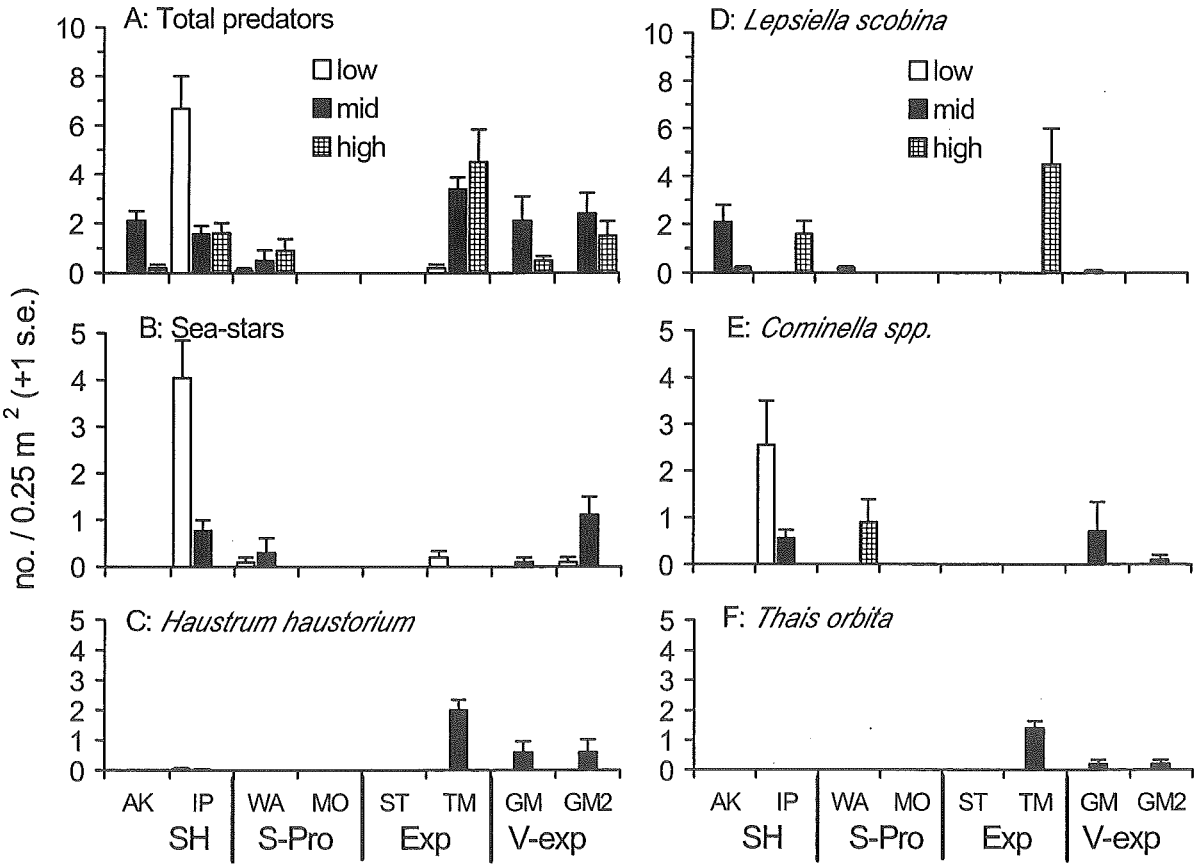

Figure 2.5. The abundance per 0.25m^2 of all predator species (A), all sea-stars (B), *Haustrum haustorium* (C), *Lepsiella scobina* (D), all *Cominella* species (E) and *Thais orbita* in the Low, Mid and High tidal zones of all sites across the four exposure levels.

2.3.3. Biomass

The total shell free dry weight of all organisms varied between sites within exposures and by tidal height (Table 2.3). The greatest biomass of organisms occurred in the low tidal zone of the semi-protected and exposed sites (Fig. 2.6A). The mid tidal zone at these sites had less than half of the low zone biomass. At the very exposed sites, the mid zone had a greater biomass than the lower and upper zones. The overall biomass of organisms with respect to exposure was greatest at the sites of intermediate exposure, which averaged *c.* 150 grams per 0.0625m^2 (i.e., 2.4 kg per m^2) compared to *c.* 90 per 0.625m^2 at the very exposed sites and *c.* 40 per 0.0625m^2 at the sheltered sites (Fig. 2.6B). Biomass did not mirror macroalgal abundance (cf, Fig. 2.2) because of the dense layering of bull kelp and fucalean species at sites of intermediate exposure. The biomass of algae varied significantly between sites within exposures and within the tidal zones of these sites (Table 2.3B). By far the greatest biomass on the semi-exposed shores was due to macroalgae (Fig. 2.6C). On exposed sites, macroalgae had over twice the weight of the filter-feeding organisms (Fig. 2.6D).

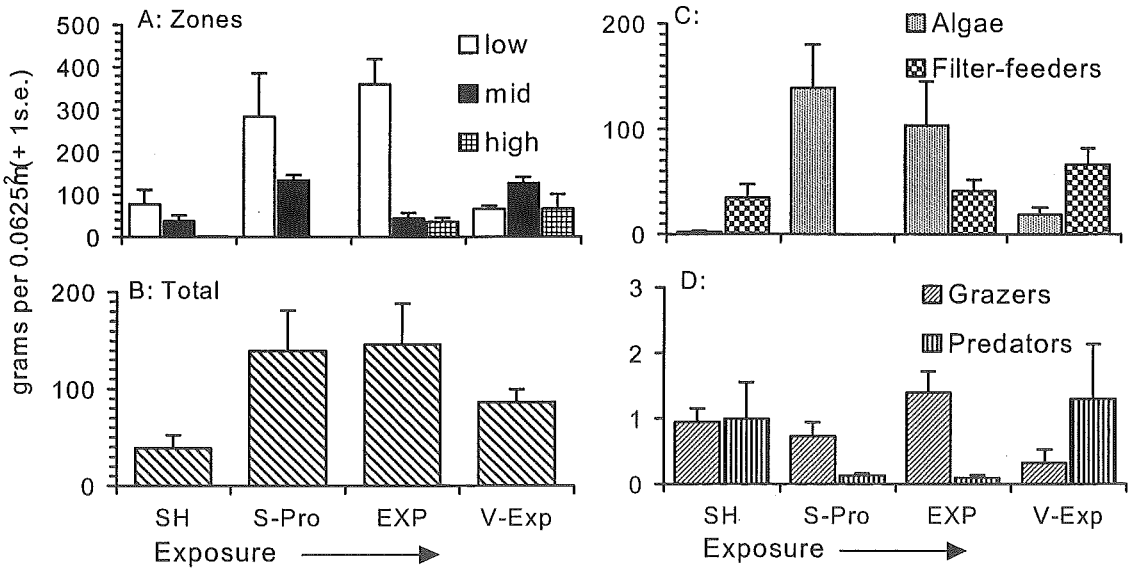

Figure 2.6. The average biomass (shell free dry weight) per 0.0625m^2 from complete clearances in the three tidal zones (A), the average total biomass (B), the biomass of all algae and filter-feeder species (C) and all grazer and predator species (D) across the four exposure levels.

Filter-feeder biomass varied considerably between sites within exposures and between tidal zones within sites (Table 2.3C), dominating the biomass of sheltered and very exposed sites. Despite their abundances, grazers and predators had relatively small weights overall (Fig. 2.5D). The biomass of predators varied significantly between sites within exposures (Table 2.3D). Their greatest biomass occurred at the sheltered and very exposed sites. Grazer biomass varied significantly between sites within zones and between tidal heights at these sites (Table 2.3E), and was greatest at the three lesser exposures.

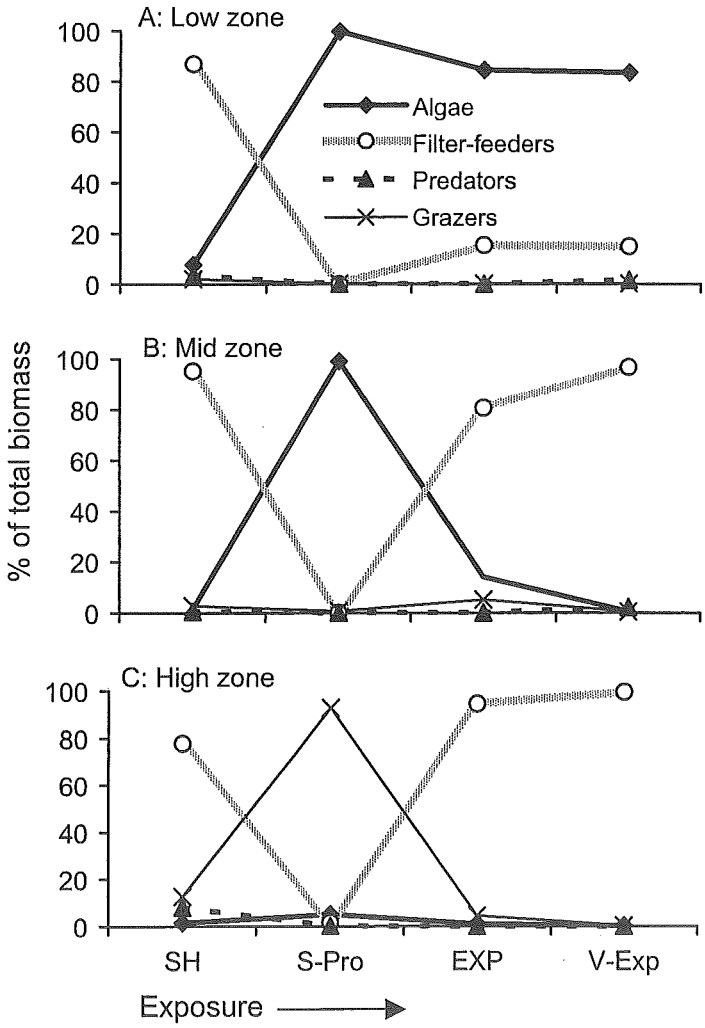

Figure 2.7. The percentage contribution of functional groups to the total biomass in the three tidal zones low (A), mid (B) and high (C) across the four exposure levels.

Table 2.3. Hierarchical analyses of variance of the effects of exposure, sites within exposure and shore zone on the average biomass (S.F.D.W.) per 0.0625m^2 of (A) total biomass, (B) algae, (C) filter-feeders, (D) predators and (E) all grazers. Some data were transformed using [1] $(x)^{0.5}$ to stabilize variances; [2] denotes cases where variances could not be stabilized and Cochran's tests were significant.

Group	Source	df	Ms	F	p
A: [2] Total biomass	Exposure	3	45340.1	3.99	0.107
	Sites (Exp.)	4	11357.2	2.23	0.080
	Shore Zone	2	180423.7	10.62	0.006**
	Exp. x zone	6	53843.6	3.17	0.675
	Sites (Exp.) x zone	8	16991.3	3.33	0.004***
	Residual	48	5104.14		
B: [2] Algae	Exposure	3	77784.8	4.64	0.086
	Sites (Exp.)	4	16770.1	3.66	0.011**
	Shore Zone	2	173929.4	11.57	0.004***
	Exp. x zone	6	44306.5	2.95	0.080
	Sites (Exp.) x zone	8	15031.2	3.28	0.005**
	Residual	48	4580.17		
C: [2] Filter-feeders	Exposure	3	13382.90	2.01	0.255
	Sites (Exp.)	4	6669.85	10.07	0.000***
	Shore Zone	2	3385.61	0.64	0.552
	Exp. x zone	6	7762.71	1.47	0.300
	Sites (Exp) x zone	8	5278.91	7.97	0.000***
	Residual	48	662.52		
D: [2] Predators	Exposure	3	6.76	076	0.572
	Sites (Exp.)	4	8.89	2.58	0.049*
	Shore Zone	2	6.67	1.28	0.328
	Exp. x zone	6	5.97	1.15	0.415
	Sites (Exp.) x zone	8	5.20	1.50	0.181
	Residual	48	3.45		
E: [1] Grazers	Exposure	3	1.19	5.97	0.060
	Sites (Exp.)	4	0.20	1.62	0.185
	Shore Zone	2	0.73	1.09	0.382
	Exp. x zone	6	0.75	1.12	0.429
	Sites (Exp.) x zone	8	0.67	5.40	0.000***
	Residual	48	0.12		

In terms of percentage composition of the biomass within shore levels and exposures (Fig. 2.7), macroalgae made up almost 100% of the biomass in the low zone at semi-protected sites and >80% of the biomass at exposed and very exposed sites, while filter-feeders made up *c.* 90% of the biomass at sheltered sites (Fig. 2.7A). In the mid tidal zone, filter-feeders made up >80% of the biomass of all exposures except at semi-protected sites, where macroalgae made up almost 100% of the biomass (Fig. 2.7B). In the upper tidal zone, filter-feeders also made up >80% of the biomass of all but semi-protected sites, where grazing molluscs formed most of the biomass (Fig. 2.7C).

2.3.4 Species Richness

The effects of exposures on the total number of all species varied with tidal zone (Table 2.4A). The greatest number of species per sample occurred in the low tidal zone of the semi-protected and very-exposed sites and in the mid tidal zone of the semi protected sites (Fig. 2.8). Generally, the lower tidal zone had more species than the mid tidal zone, which in turn, had more species per sample than the upper tidal zone. However, at the semi protected sites the mid zone had more species per sample than the low zone. The number of species per sample in the upper tidal zone of the exposed and very-exposed sites was twice that of the sheltered and semi-protected (Fig. 2.8A). The overall average number of species per sample was greatest at the semi protected and very-exposed sites, which averaged *c.* 20 species per $0.0625m^2$ compared to *c.* 12 species per $0.0625m^2$ at sheltered sites and *c.* 16 species per $0.0625m^2$ at the exposed sites (Fig. 2.8B). Macroalgae accounted for the greatest number of species per clearance on the semi-exposed shores, while filter-feeders accounted for less than a quarter of the species per sample at these sites (Fig. 2.8C).

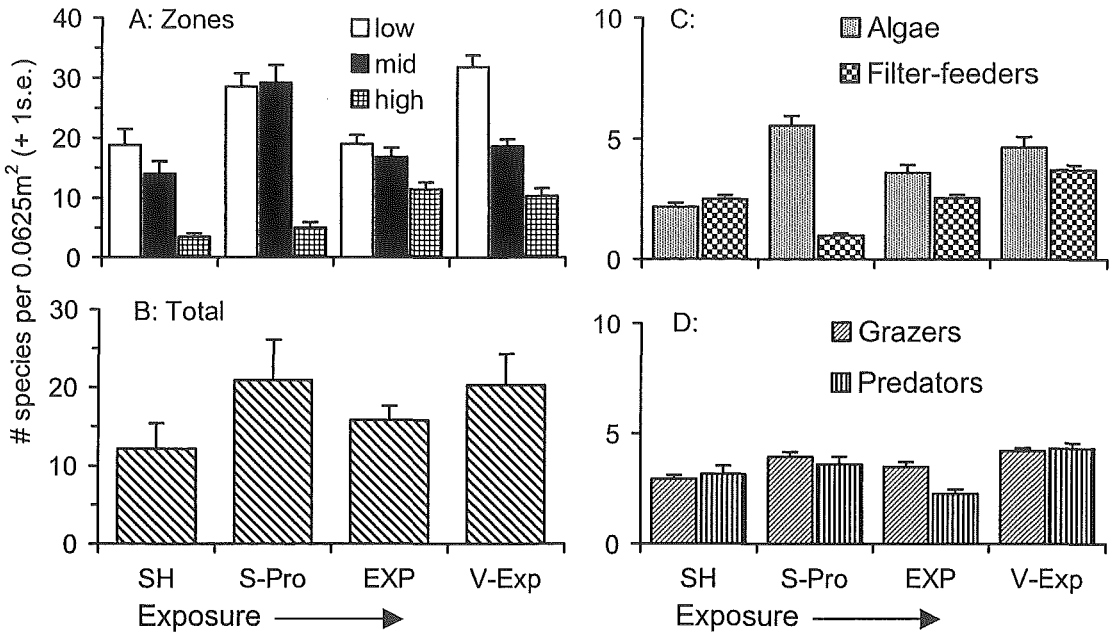

Figure 2.8. The average number of species per 0.0625m² in the three tidal zones (A), the average total number of species (B), of all algae and filter-feeders (C) and all grazers and predators (D) across the four exposure levels.

On average, at sheltered sites there were more filter-feeding species per sample than species of macroalgae. At all other exposures there were greater numbers of algae species than filter-feeder species per 0.0625m² clearance. The number of grazer and predator species per clearance varied considerably between sites within exposures and within the shore zones at these sites (Table 2.4D and 2.4E). The average number of grazer and predator species per clearance was similar across all exposures (Fig. 2.8D), but they were most diverse at the very exposed sites. In terms of percentage composition of total species richness per sample within shore levels and exposures (Fig. 2.9), macroalgae made up *c.* 35% of the species richness in the low zone at the semi-protected, exposed and very exposed sites while all groups contributed to the species richness at sheltered sites (Fig. 2.9A). In the mid tidal zone, predator and grazer species combined to account for *c.* 65% of the species richness at the sheltered sites. At the semi-protected sites macroalgae, grazers and predators combined to account for *c.* 95% of the total species richness. At the exposed sites grazer species alone accounted for

30% of species richness because of the large number of cryptic grazers found in clearances and at the very exposed sites predator and filter-feeder species combined to make up *c.*65% of the total species richness (Fig. 2.9B). In the upper tidal zone, grazers, in particular, grazing molluscs made up >30% of the total species richness per sample at all sites (Fig. 2.9C).

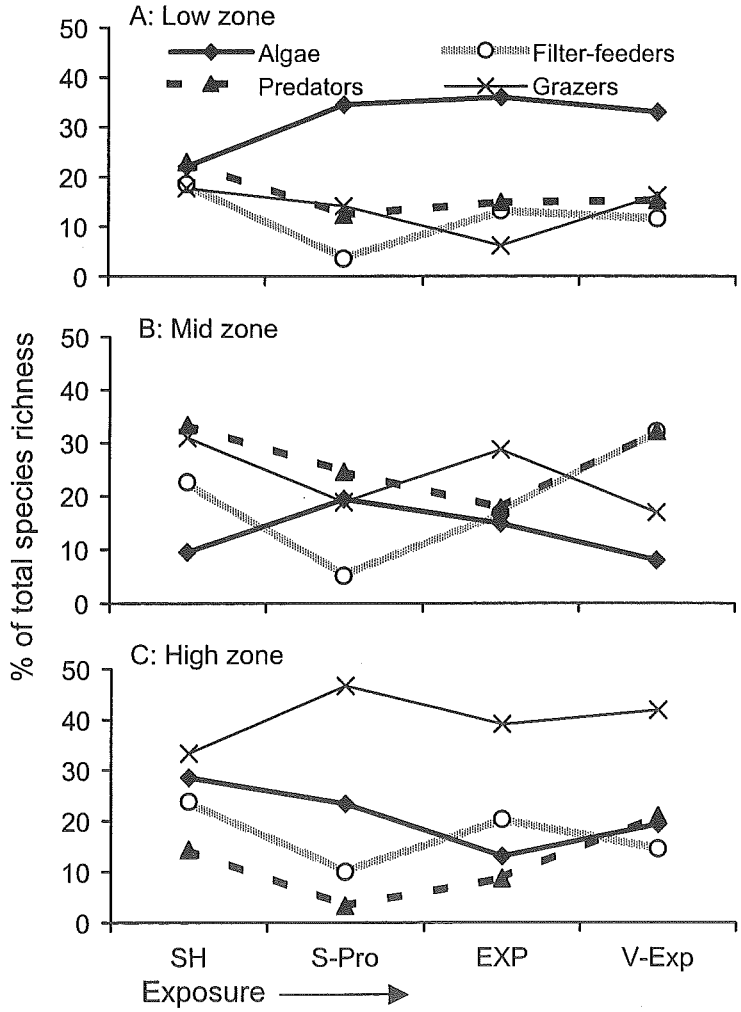

Figure 2.9. The percentage contribution of functional groups to the total number of species in the three tidal zones low (A), mid (B) and high (C) across the four exposure levels.

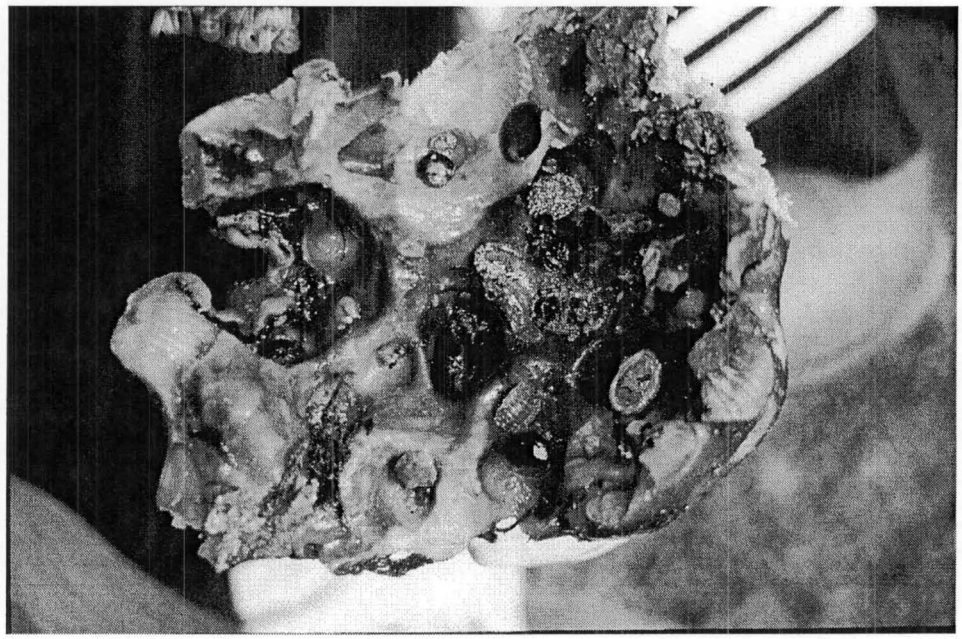

Figure 2.10. A picture of a *Durvillaea antarctica* holdfast with a diverse range of infauna, mainly cryptic grazer species like chitons *Amaurochiton glaucus, Acanthochiton zealandica, Onithochiton neglectus* and the pulmonate limpet *Siphonaria australis.*

Table 2.4. Hierarchical analyses of variance of the effects of exposure, sites within exposure and shore zone on the average species richness per 0.0625m^2 of (A) total species, (B) algae, (C) filter-feeders, (D) predators and (E) all grazers. All Cochran's tests were not significant.

Group	Source	df	Ms	F	p
A: Total species	Exposure	3	305.90	3.03	0.156
	Sites (Exp.)	4	101.07	8.57	0.000***
	Shore Zone	2	1829.43	76.14	0.000***
	Exp. x zone	6	156.82	6.53	0.009***
	Sites (Exp.) x zone	8	24.03	2.04	0.061
	Residual	48	11.79		
B: Algae	Exposure	3	53.38	4.34	0.095
	Sites (Exp.)	4	12.30	6.06	0.000***
	Shore Zone	2	285.51	102.27	0.000***
	Exp. x zone	6	17.55	6.29	0.010**
	Sites (Exp.) x zone	8	2.79	1.38	0.231
	Residual	48	2.03		
C: Filter-feeders	Exposure	3	22.41	3.09	0.152
	Sites (Exp.)	4	7.25	8.42	0.000***
	Shore Zone	2	26.93	13.19	0.000***
	Exp. x zone	6	6.00	2.94	0.080
	Sites (Exp) x zone	8	2.04	2.37	0.031*
	Residual	48	0.86		
D: Predators	Exposure	3	13.31	0.35	0.792
	Sites (Exp.)	4	37.93	15.01	0.000***
	Shore Zone	2	113.40	14.00	0.002**
	Exp. x zone	6	7.63	0.94	0.515
	Sites (Exp.) x zone	8	8.10	3.20	0.005**
	Residual	48	2.53		
E: Grazers	Exposure	3	36.05	1.86	0.278
	Sites (Exp.)	4	19.43	9.65	0.000***
	Shore Zone	2	64.22	7.43	0.015**
	Exp. x zone	6	29.48	3.41	0.056
	Sites (Exp.) x zone	8	8.64	4.29	0.001**
	Residual	48	2.01		

2.3.5 *Overall Patterns*

Combined results of the percentage cover data provide a general impression of the dominance of the habitat-forming groups of algae and filter-feeders, and the amount of bare space available across exposures (Fig 2.10A). In general, the amount of bare space was greatest at the sheltered sites and least at the semi-protected and exposed sites but increased slightly at the very exposed sites. Macroalgae were more abundant than filter-feeders at the semi-protected sites. At all other levels of exposure filter-feeders were more abundant than macroalgae. The average abundance of predators per m^2 over exposures followed a bimodal distribution and were most abundant at the sheltered and exposed sites with between *c.* 200-300 per m^2 (Fig. 2.10B). Grazers were most abundant at the exposed sites reaching densities of 300 per m^2, at the all other site grazer were present at between 50-100 per m^2.

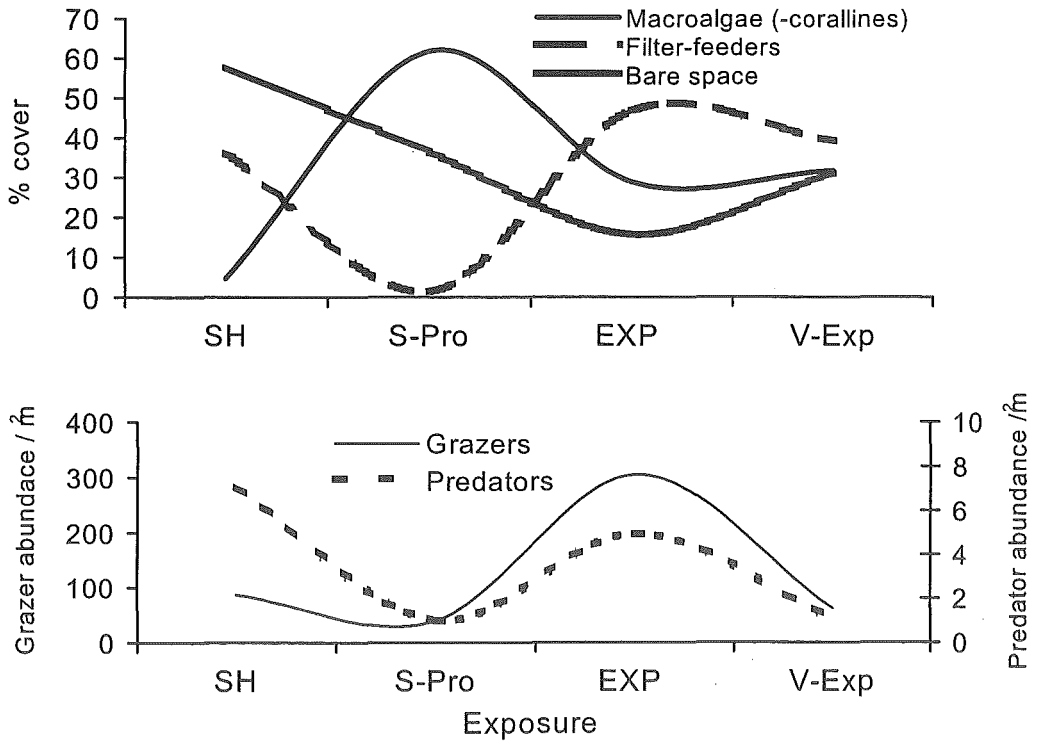

Figure 2.11. The total pattern of percentage cover of macroalgae and filter-feeder assemblages, and bare space (A), and the average abundance of grazers and predators per m^2 (B), across the four exposure levels.

2.4. Discussion

An analysis of patterns in habitat associations, biomass and species richness within and between four levels of wave exposure through quantitative sampling within tidal zones at eight intertidal rocky platforms in southern New Zealand revealed significant differences within and between sites and zones within sites. Of particular interest were patterns in habitat-forming algae and filter-feeder species across wave exposure gradients. Associated with habitat-forming species were clear patterns in biomass. Generally, algae dominated the lower tidal zone in terms of biomass and percentage cover at all but the most sheltered sites. The biomass of this tidal zone was greatly influenced by the presence of the large 'Bull kelp' *Durvillaea antarctica* at semi protected and exposed sites. The mid tidal zone biomass was most often dominated by mussels, particularly the blue mussel *Mytilus galoprovincialis* and the green-shell mussel *Perna canaliculus*. At semi-protected sites the biomass in this zone was dominated by perennial brown algae such as *Hormosira banksii* and *Cystophora torulosa*. Barnacle assemblages, particularly *Chaemosipho* species and *Epopella plicata* dominated biomass in the upper tidal zones at wave exposed sites. Associated with all habitats were large numbers of invertebrate grazers, particularly in the upper tidal zones of the exposed and very exposed sites. Coralline algae were most abundant in the lower and mid tidal zones and were associated with algal dominated habitats.

These data are important because the intertidal shores of New Zealand have been used to test major ecological theories and paradigms and are often compared and contrasted to North American shores. For example, Paine (1971) presented evidence of parallel processes acting in different hemispheres when he showed that the starfish, *Stichaster australis*, maintained a band of bull kelp, *Durvillaea antarctica*, by preventing the mussel, *Perna canaliculus*, a 'competitive dominant' from dominating space in the low tidal zone at a site on the west coast of northern New Zealand. He compared the *Stichaster/ Perna/ Durvillaea* predation linkage to that of the starfish *Pisaster ochraceus* and the mussel *Mytilus californianus* at Mukkaw Bay, Washington and suggested that

both starfish were 'keystone species' capable of maintaining greater diversity in an assemblage by preferentially removing competitively dominant mussels. Recently, linkages between nearshore oceanographic conditions and on-shore processes in the intertidal of New Zealand were and compared to those found on the west coast of North America (Menge et al. 1999). They state that more persistent upwelling on the West coast causes greater mussel recruitment, and therefore greater effects of predation compared to the East Coast of the South Island. Unfortunately, compared to the prodigious number of studies documenting the patterns and processes affecting communities on North American intertidal shores there is a paucity of quantitative data of patterns in abundance of key intertidal species over large spatial scales in New Zealand. The quantitative data presented here help provide a framework from which further hypotheses about the processes structuring intertidal communities on New Zealand's shores can be produced.

Habitat-forming Filter-feeders and Macroalgae

Macroalgae and filter-feeding species can dominate large areas of the intertidal zone. I found that assemblages of filter-feeder were abundant across all tidal zones at the two sheltered sites and the exposed site at Taylor's Mistake and were abundant in the mid and upper tidal zones of the very-exposed sites. However, filter-feeder assemblages were scarce at the semi-protected sites.

Many filter-feeding species, particularly mussels and barnacles, have been labelled competitive dominants by other studies (Paine, 1971, 1974; Menge and Farrell, 1989). Provisional evidence of competitive dominance might be a lack of bare substratum. However, in the current study the amount of bare substrate was highly variable and depended on exposure, site and tidal zone. A reduced amount of bare substrate could be attributed to filter-feeding assemblages in the mid tidal zones of Taylors Mistake and Greymouth 2, where the mussel *Mytilus galloprovinicalis* dominated. Also, in the upper tidal zones of the exposed and very-exposed sites where

the barnacles *Epopella plicata*, *Chaemosipho columna* and *C. brunaea* and the nesting mussel *Xenostrobus pulex* dominanted. Macroalgae dominated more than eighty percent of the cover in the lower tidal zone at the semi-protected, exposed and very-exposed sites and in the mid tidal zone at the semi-protected sites.

The changes in patterns of habitat dominance across wave exposures allows several hypotheses to be generated. In general, coralline algae were not associated with filter-feeder habitats but were associated with macroalgae. It could, therefore, be hypothesized that coralline algae negatively affect the recruitment of filter-feeder assemblages, and positively affect the recruitment of habitat-forming large brown and red algae at these sites. Several studies have found that coralline algae can both facilitate and inhibit recruitment in intertidal habitats. For example, on the exposed coast of Washington Suchanek (1978) found *Mytilus edulis* could occupy space in a zone otherwise dominated by *Mytilus californianus* by settling into coralline algae. Geniculate coralline algae and the microhabitat they produce have been found to facilitate the recruitment of fucoid algae (Brawley and Johnson, 1991,1993; Benedetti - Cecchi and Cinelli, 1992). In contrast, Camus (1994) found non-geniculate coralline algae, through the shedding of epithallial cells, reduced the recruitment of *Lessonia nigrescens* in Chile. Coralline algae could, therefore, play a major role in determining assemblages on these shores. Experiments examining the pre-emptive ability of coralline algae across habitats and wave exposures could evaluate the importance of these interactions.

Alternatively, demographic processes could determine the abundance of filter-feeder assemblages at the semi-protected sites in this study. One alternative hypothesis is that the supply of larvae is restricted by the frequency of upwelling of oceanic water masses (Menge et al., 1999). Menge et al. (1999) suggest that the dominant downwelling conditions on the east coast of southern New Zealand may affect the supply of filter-feeder larvae at many sites. However, because of the large scale of upwelling events and the great number of confounding variables that are related to such scales many of the

hypotheses generated by Menge et al. (1999) can not be tested experimentally. Therefore, in order to understand the importance of processes like upwelling to the structure of intertidal assemblages marine ecologist are reliant on correlative links between larval supply, nearshore oceanographic conditions and onshore community structure. Future experimental studies at sites with and without filter-feeder assemblages on the east and west coast of New Zealand could increase our understanding of the importance of demographic process in structuring these habitat-forming communities.

Patterns in the abundance of species of macroalgae across exposures were found. Key habitat-forming algae in the low tidal zone of one of the semi-protected and both exposed sites were *Durvillaea antarctica*, *Carpophyllum macshalocarpum*, *Cystophora torulosa* and *Cystophora scalaris*. At the very-exposed sites a number of red algae in the genus *Gigartina* dominated the lower tidal zone. The perennial fucoid *Hormosira banksii* was the most abundant alga in the mid tidal zone, dominating large areas of the semi-protected sites.

Because habitat-forming algae provide a significant proportion of the biomass on intertidal shores the processes determining their distribution and abundance can have significant consequences for the flow of nutrients through communities at different wave exposures. For example, *D. antarctica* dominated biomass in the lower tidal zone at semi-protected and wave exposed sites in my study but was absent at sheltered sites. It may be that this major biomass contributor is unable to recruit into non-geniculate corallines, or it may become physiologically stressed in more sheltered situations. The processes determining the vertical distribution of *D. antarctica* have been explored by Hay (1979) who found that *D. antarctica* can recruit higher on the shore if limpets are removed but its vertical distribution is eventually determined by desiccation stress. Little is know of the processes determining its distribution along the shore. However, once established adult plants of *D. antarctica* appear to exclude other species of algae and mussels through shading and abrasion (c.f. Kennelly, 1987; Reed

and Foster, 1984; Schiel, 1988). For example, Paine (1971) suggested the absence of *Perna canaliculus* under canopies of *D. antarctica* even when predatory starfish had been removed was related to the large blades battering mussels or inhibiting larval settlement and recruitment. Experiments along gradients in wave exposure are necessary to determine the processes affecting the distribution of this key species.

Another important pattern I observed was that *Hormosira banksii* and *Cystophora* species are able to grow in more sheltered situations despite greater sedimentation. Several studies have explored the effects of sediments in determining algal community structure elsewhere (e.g. Devinny and Volse,1978; Airoldi and Cinelli, 1997; Madsen et al., 2000). For example, Devinny and Volse (1978) found that $<$1mm of sediment could prevent the successful attachment of *Macrocystis pyrifera* germlings in the laboratory. In New Zealand, Schiel et al. (In review) found that small amounts of sediment may facilitate recruitment of algal germlings by providing protection from sedimentation but large amounts of sediment eventually smothered recruits. Experiments testing the relative abilities of early life stages of these species to survive and grow when exposed to similar levels of sedimentation are necessary to determine the importance of this process.

Grazers and Predators

I found considerable variation in the number of invertebrate predators and grazers, both small and large, between sites within exposures and between tidal zones. However, in general because cryptic grazers were abundant at all sites there was no difference in the abundance of invertebrate grazers across wave exposures. Large grazers, particularly Cellana ornata, were abundant in the upper tidal zone at the exposed sites and *Turbo smaragdus* and *Chiton pelliserpentis*, were abundant at in the low tidal zone of the sheltered Island point site. Small grazers were abundant in the high tidal zones among filter-feeder assemblages on the more exposed sites and no doubt influence the recruitment of algae into these habitats. Predators, in particular the

starfish *Patiriella regularis* and whelk *Cominella maculosa*, were abundant at the sheltered Island point site and may affect the recruitment of mussel assemblages at this site.

Predation and grazing are important structuring processes in intertidal assemblages and can affect patterns of horizontal and vertical distribution and abundance (eg. Hawkins and Hartnoll, 1983; Underwood, 1984; Menge et al. 1994). Their affect on the structure of assemblages can vary with the size of the prey, the abundance of predators and grazers and their ability to effectively graze or prey upon organisms under variable environmental conditions (Paine, 1974; Lubchenco, 1978, 1983; Menge, 1978a, 1978b, 1983; Underwood, 1980; Menge et al., 1994). Grazer and predator effectiveness can also depend on factors like the heterogeneity of the substrate, their method of feeding, the ability of the prey to withstand or evade grazing and predation and the amount of environmental disturbance (Menge and Sutherland, 1976; Lubchenco, 1983; Underwood and Jernakoff, 1984; Paine et al., 1985). The effects of predators and grazers on intertidal assemblage structure can be substantial and a paucity of macro-algae on many shores has been reversed through the removal of grazers (e.g. Lubchenco, 1983; Hawkins and Hartnoll, 1983).

Patterns in the abundance and effectiveness of grazer and predator species within habitats have been hypothesized to vary with wave exposure (Menge and Sutherlands, 1987). In my study, I found no difference in the abundance of associated grazers and predators among wave exposures. This was largely due to greater numbers of cryptic grazers, like *Chiton pelliserpentis*, under holdfasts and in cracks and crevices at more exposed sites. Experiments examining the relative ability of grazers to affect the recruitment of early life stages of key habitat-forming species across wave exposures are detailed in later chapters.

Biomass

Patterns of intertidal biomass and species richness across exposures have been illustrated in a number of studies (McQuaid and Branch, 1984, 1985; Menge and Sutherland, 1976, 1987; Kilar and McLachlan, 1989; Bustamante and Branch, 1996; Bustamante et al., 1997). McQuaid and Branch (1984) found biomass of assemblages dominated by filter- feeders increased with wave exposure on South African shores. In my study, I found that the effects of tidal height on the biomass of filter-feeders varied with site but overall their biomass increased as exposure increased particularly in the upper tidal zone. This pattern is probably influenced by the ability of filter-feeder assemblages to recruit and survive higher on the shore with greater wave action but the links between nearshore productivity, oceanographic conditions and the pathways that lead to greater biomass in exposed conditions await further experimental evaluation.

Species richness

Species diversity is often used by ecologists to describe community structure but the reasoning behind it's use is often unclear. Studies of small-scale diversity changes have produced evidence that diversity can vary as a result of several factors including the abundance of consumers and the frequency of disturbances (Lubchenco, 1978; Sousa, 1979; Petraitis et al., 1989), the abundance of key resources (Seed, 1996), environmental conditions (Kautsky and Kautsky, 1989; Kilar and Mclachlan, 1989) and specific features of the local environment (Thompson et al., 1996; Trowbridge et al., 1996). However, there are three major problems faced by those wishing to study species diversity. First, quantifying observed differences in diversity is complicated by the size of the sample area and the magnification used to sort it because the closer you look the more species you find. Consequently, scarce species and species in micro-habitats are often missed. Second, a complex interaction of factors creates and maintains variations in species diversity. Finally, it is possible that differences in local-

scale diversity may have little ecological meaning and may simply be a complicated construct of ecologists (Valiela, 1995).

A number of diversity indices have been used to analyse species diversity data in ecology. Examples include Simpson's index (D), the Shannon - Weaver index (H') and the index of species richness (R). Each has drawbacks and measures a slightly different aspect of diversity. As a result, different trends can be found depending on the index used. For example, when testing predictions of Connells (1978) Intermediate Disturbance Hypothesis on a rocky reef in Caribbean Panama, Kilar and McLachlan (1989) found species richness (R) to be less variable within habitats than measures of diversity (H') and eveness (J').

In my study, I used species richness to compare communities across wave exposures. Species richness not significantly different across wave exposures. However, complete clearances did allow a better estimation of the abundance of cryptic invertebrate grazers and predators often missed by percentage cover estimates. Further studies examining the patterns of species at different scales, and across habitats, may be useful in understanding the role of functional group diversity in determining the resistance and persistence of intertidal assemblages to disturbances at microscopic and macroscopic levels.

Wave exposure

I use wave exposure to describe the wave climate of a site as quantified by the use of dynamometers. Before dynamometers and more complex electronic equipment, early studies used biological wave exposure scales. By monitoring the presence and abundance of certain indicator species, these scales provided a cheap and relatively effective method of assessing the wave climate (Ballintine, 1961; Dalby et al. 1978; Dalby, 1985). However, the inherent problem of circularity and the ambiguous nature of the term means biological wave exposure scales are not intended to be, and cannot

be, used to explain the processes responsible for horizontal distribution patterns (Ballintine, 1961).

More recent studies of horizontal distribution and biogeographic patterns have concentrated on correlating the effects of wave exposure, substratum, sea-surface and substrate temperature and oceanographic conditions with the trophic structure, biomass and species richness of intertidal shores (e.g. Bustamante and Branch, 1996; Bustamante et al., 1997; Menge et al 1999). However, the large geographic distances encompassed by these studies incorporate many between-site differences in local climate, oceanographic conditions, substrate, sedimentation, rainfall, salinity and other environmental variables. Consequently, when testing the processes responsible for such patterns efforts must be made to control for as many of these variables as possible.

Summary

In this study I used sites separated by large geographic distances and of distinct wave exposure to illustrate patterns in the abundance of habitat-forming species and associated species. Despite large between-site differences in variables like substrate, oceanographic conditions and local climate distinct patterns in habitat-forming macroalgae and filter-feeding assemblages were found. These results suggest that experiments examining the specific responses of early life-stages of habitat-forming species to a range of biological and environmental processes will benefit from being done at several spatial scales. Such studies will allow many of the important processes that are responsible for these patterns along intertidal gradients to be determined.

Chapter 3

EARLY POST-SETTLEMENT STAGES OF HABITAT-FORMING ALGAE ACROSS EXPOSURES

The importance of 'stickability'

3.1 Introduction

The ability of early life stages to remain attached to rocky substratum following settlement is fundamental in determining the distribution and abundance of benthic populations. Of the numerous environmental and biological factors that affect the distribution and abundance of intertidal populations wave action is one of the more important and has received much attention over the last twenty years (Hurd, 2000). The combined indirect and direct hydrodynamic effects of wave action on nearshore intertidal biota are often grouped under the term 'wave exposure' (Ballantine, 1961; Dalby et al., 1978; Menge and Sutherland, 1987; Denny, 1995). Direct effects of wave forces on intertidal organisms can include damage, detachment and displacement (Vogel, 1984; Denny, 1995). Indirect effects can involve interactions with sediment, logs, rocks and adult populations (Dayton, 1971; Paine and Levin, 1981; Sousa, 1984; Schiel 1985; Schiel, 1988). Competition within and between species and predation across exposures form the basis of models of on-shore processes (Connell, 1961; Menge, 1978; Menge and Sutherland, 1987; Menge and Farrell, 1989; Menge et al., 1994). Until recently, however, many of the specific processes linking patterns of species distributions and abundance to wave action had not been quantified or examined experimentally (Vadas et al., 1990; Denny, 1995).

Significant progress has been made in understanding the effects of wave forces on the size, distribution and abundance of larger recruit and adult stages of intertidal organisms (e.g. Koehl, 1984; Vogel, 1984; Denny et al., 1989; Denny, 1987; Carrington,

of mucilage could benefit epiphytic species or those species settling in high wave-energy environments. Moorjani and Jones (1972) found that the epiphytic coralline alga *Jania* had a stronger and faster attachment than did the benthic *Corallina officinalis.* Similarly, the slow and weak attachment of early life stages of the large brown alga *Ascophyllum nodosum* may explain its absence from high wave energy situations (Vadas et al. 1990).

There are clear differences in the dominant habitat-forming algae across exposures on the intertidal platforms of the eastern coast of southern New Zealand (Morton and Miller, 1971; Schiel and Taylor, in prep.). In wave-exposed situations, the dominant alga is the large bull kelp *Durvillaea antarctica* (Chamisso) Hariot (Family Durvillaeales), the biomass of which can reach 80 kg per m^2. However, the distribution of *Durvillaea* does not extend to more sheltered shores, which instead are dominated by fucalean algae such as *Cystophora torulosa* (R. Brown) J. Agardh on the lower shore and *Hormosira banksii* (Turner) Descaisne on the mid shore. With the exception of small plants in cracks and tide pools (Osborn, 1948), *H. banksii* and C. torulosa are not found in wave-exposed situations.

The upper intertidal zone along much of the north west coast of U.S.A. and in British Columbia is occupied by a mosaic of perennial macroalgae and barnacles (Ricketts et al. 1969). However, mono-specific stands of fucoid algae can be found in relatively wave sheltered sites (Cubit, 1984; Kim and De Wreede, 1996). The most common fucoid algae on these shores are *Pelvetiopsis limitata* Gard and *Fucus gardneri* Silva and several studies have shown that the microhabitat provided by barnacles facilitates the recruitment of these algae (Cubit, 1984; Kim and De Wreede, 1996; Kim, 1997). Small plants of both species persist even in wave exposed situations. Recently, Blanchette (1997) showed, by transplanting plants across wave exposures in Oregon, that the size of plants of *Fucus gardneri* at exposed points was largely determined by the pruning effects of wave action on recruits and adults.

This study examines the possibility that the observed patterns of distribution and abundance of habitat-forming large brown algae are related to the ability of their zygotes

to stick and remain attached when exposed to varying degrees of water motion. I test the hypothesis that zygotes of *Cystophora torulosa* and *Hormosira banksii*, characteristic of more sheltered situations, will not attach as quickly and will not survive wave action as well as the exposed-shore species *Durvillaea antarctica*. I test this hypothesis under artificial and natural wave conditions and over various post-settlement times. For comparison, the ability of two species of fucoid algae, *Fucus gardneri* and *Pelvetiopsis limitata*, to stick and remain attached, in Oregon U.S.A., was also tested across exposures.

3.2 Materials and methods

In this study I did two sets of experiments. The first of these were "single-wave" experiments, done in both the laboratory and the field. These tested the immediate consequences of the least amount of wave action on the ability of algal zygotes to remain attached. These were done as a comparison with another published study on algal zygote attachment (Vadas et al., 1990). The second set of experiments ("full tidal cycle") were done in the field and tested the consequences of different setting times and levels of wave action on the survival of zygotes over a complete tidal cycle (approx. 12 hr.). In all experiments, I refer to "survival" as zygotes remaining attached to experimental surfaces. Initially, detachment may not be fatal but at later stages detachment from the substratum is almost certainly fatal for developing zygotes because they have little or no ability to re-attach.

3.2.1. Study sites

All laboratory work was done in our experimental algal facility at the University of Canterbury Field Station in Kaikoura. The field site for the single-wave experiments was a sheltered reef (Lab Rocks) in front of the field station (42°25'S, 173°41'E; see chapter 1, Fig. 1.5B). The second set of experiments was done at two sites within each of three categories of wave exposure around the Kaikoura peninsula and at two sites on the central Oregon coast (see chapter 1, Fig. 1.6). Both areas have sites of a wide range of exposures to

wave action, from sheltered sites in the lee of headlands protected from oceanic swells, to very exposed sites continuously exposed to oceanic swells. The wave exposure categories were Sheltered, Intermediate and Exposed. They were selected on the basis of other work we have done within these sites in which dynamometers were used (Bell and Denny, 1991) and on the predicted direction of swell for the twelve hours of the experiment (Meteorological Service Report).

Within both sets of experiments, there were two runs, comparing species with different reproductive periods (see below). However, in the second set of experiments (those lasting 12 hr), we were unable to use the same sites for both runs. This was because of a change in direction of the predicted swell and also a spill of eight tonnes of rat poison that prevented access to some of the sites. For both sets of experiments, sheltered sites had a range of wave heights between 5-20 cm; intermediate sites had between 30-50 cm and exposed sites between 100-150 cm.

3.2.2. Species studied

We used different combinations of species in our experiments. This was dictated by the reproductive periodicity of the species. *Durvillaea antarctica* is a dioecious species that releases gametes naturally over a 16 week period during winter (May -August) (Hay, 1979b; Clayton, 1990). Raised male and female conceptacles scattered over the blades identify reproductive plants (Adams, 1994). *Hormosira banksii* is a perennial, dioecious, fucalean alga that dominates the middle to lower shore on many sheltered and intermediately exposed platforms. Populations release gametes throughout the year, but there are large pulses during the warmer months (September - April) (Schiel. unpublished data). *Cystophora torulosa* is a perennial, monoecious, fucalean alga that reproduces in pulses in spring and summer (September - January). *Fucus gardneri* is a monoecious, perennial fucoid alga that reproduces during the northern hemisphere spring, summer and early autumn (Abbott and Hollenberg, 1976). *Pelvetiopsis limitata* is a hardy high shore perennial alga that is monoecious and also reproduces during spring, summer and early

autumn in the northern hemisphere (Abbott and Hollenberg, 1976). All five species usually fertilise externally, which seems to occur quickly after gamete release. There is no obligate planktonic developmental stage for these species.

During austral winter of 2000 and 2001 (for *Durvillaea antarctica* and *Hormosira banksii* experiments), austral spring and summer 1999 / 2000 (for *Hormosira* and *Cystophora torulosa* experiments), and boreal summer 2001 (*Fucus gardneri* and *Pelvetiopsis limitata*) reproductive plants were collected in the field and returned to the laboratory where they were refrigerated at 4°C for 24 hours. Exposing plants to sunlight and warmth initiated gamete release. Gametes were washed from the adult plants using seawater, concentrated in glass beakers and left for 15 minutes to allow fertilisation. The zygote suspension was then poured gently over plates covered with 1cm of seawater. Approximately 100 plates per species were seeded for each experiment in large plastic trays at different time periods.

3.2.3 Experimental Design

Fibre-based cement plates were used as a standard synthetic substratum for settlement. We have used these in numerous experiments and found them to have favourable water holding and attachment properties. Plates were 7 mm thick and were cut into 5cm x 5cm squares. The plates were soaked in seawater for 24 hours prior to settling with zygotes. Three settlement times were used. In all cases, plates were settled with zygotes in separate batches 12 hours, 6 hours and 1 hour before beginning of each experiment to represent the range of times within a full tidal cycle. Before and after each experiment, the number of zygotes on each plate was estimated by viewing the damp plate beneath a dissecting microscope and counting five random 1 cm^2 quadrats. Counts were done 15 minutes prior to the start of the experiment. At which time water covering the plates was siphoned from the trays and plates were carefully lifted to the microscope. Plates remained damp throughout the counting process. We aimed for a settlement

density of 500-1000 cm^{-2}. Percent survival was calculated as the average number of zygotes remaining attached for each plate.

The first set of experiments (single-wave) tested the relative ability of zygotes of the three species to remain attached after different post-settlement times when exposed to an artificial standard wave in the laboratory and a single natural wave in the field. The single-wave experiment was done twice, once using *Hormosira* and *Cystophora* in Summer 1999/2000 and once using *Hormosira* and *Durvillaea* in Winter 2000. The artificial standard wave was created in the lab using a twenty-litre wave bucket (design described in Vadas et al, 1990) attached to the end of a glass-lined flume, which was 60 cm wide and 2 m long. By tipping the bucket, a wave about 5 cm high washed along the flume. Three replicate plates of each species from each post-settlement time period (1, 6, or 12 hours) were positioned randomly in the centre of the flume and then exposed to a standard wave. This was repeated three times. On the same day, another three replicate plates of each species from each post-settlement time were taken to a nearby field site (Lab Rocks) and exposed to one natural low-energy (c. 5-10cm) wave. To standardise their exposure, the plates were randomly positioned on a slotted plywood board that held them in place (as for Vadas et al. 1990). The board was then held against the shore and one low energy wave was allowed to wash over it. Again, this was repeated three times. After being exposed to waves in the laboratory and in the field, attached zygotes remaining on each plate were counted.

To control for the effect of handling plates and transferring them to treatments, three seeded control plates for each species and post-settlement time were removed from their settlement trays and placed on the outside of the flume for the same length of time that treatment plates were out of water. All of these control plates had 100% survival.

The second set of experiments done over a 12-hr tidal cycle, tested survival after different setting times over three exposure levels, using four species. During summer 2000/2001 for *Hormosira banksii*, autumn 2001 for *Durvillaea antarctica* and U.S. summer 2001 for *Pelvetiopsis limitata* and *Fucus gardneri* fibre cement plates (10 x 10 cm) were

settled with zygotes for each of three periods (1, 6 and 12 hours), as in the first set of experiments. Two low-shore sites within three levels of wave action around Kaikoura peninsula were used in New Zealand (General Introduction, Fig. 1.5B) and in Oregon two sites were used (Fogarty Creek and Depoe Bay, Fig 1.6) and three level of wave action chosen within each. The plates were taken to field sites, attached in random positions and left for 12 hours before being retrieved. The number of zygotes on each plate was counted before and after placement in the field. After the plates were counted they were kept for a further 24 hrs in seawater to assess viability of zygotes. For *Hormosira banksii*, the sheltered sites were at Lab rocks and Mudstone Bay, the intermediate sites were at Car Park and Jimmy's Beach and the exposed sites were at Second Tunnel and First Bay. For *Durvillaea antarctica*, sheltered sites were at Wairepo Beach and Mudstone Bay, intermediate sites were at Car Park and Esplanade Rocks, and exposed sites were at Seal Reef and First Bay. In Oregon, three replicate runs of the *Pelvetiopsis limitata* and *Fucus gardneri* experiment were done over three twelve hour periods at the same three points (representing three levels of wave action) at Depoe Bay and Fogarty Creek. Dynamometers were used to test relative maximum wave forces at each point at both sites.

Data were tested for homogeneity of variances using Cochran's test prior to Anova and were transformed when necessary. These tests were non-significant unless otherwise stated. In cases where the variances could not be equalised (see Results), results should be cautiously interpreted (c.f., Underwood, 1997). Analyses were done using the General Linear Model package in Statistica 6.0 (Statsoft Inc.).

3.3 Results

3.3.1 Single-wave experiments

In the single-wave experiment using *Hormosira banksii* and *Cystophora torulosa*, the duration of the post-settlement period had a significant effect on the survival of zygotes of both species when exposed to a single low-energy wave in the laboratory and in

the field (Table 3.1A, B). The species had similar survival within each post-settlement category in the laboratory. When given 1 hr to attach, only an average of 18 - 21 % of *Cystophora* and *Hormosira* zygotes remained attached (Fig. 3.1A). After a post-settlement time of 6 hr, survival improved to an average of 45 - 65 %, and after 12 hr to 85 - 95 %. The result was more complicated in the plates exposed to a single wave in the field. There was a significant interaction between species and post-settlement time (Table 3.1B) because of the relatively poor survival of *Cystophora* at 6 hr (Fig. 3.1B). In the 1 hr and 12 hr treatments, *Cystophora* averaged about 10 % greater survival than *Hormosira*. *Hormosira* averaged 40 %, 85 % and 91 % survival after 1, 6 and 12 hr of post-settlement time. During the same post-settlement periods, *Cystophora* averaged 51 %, 26 % and 99 % survival. The poor survival of *Cystophora* at 6 hr is an unexplained anomaly. Both species tended to have greater survival in the field than in the laboratory.

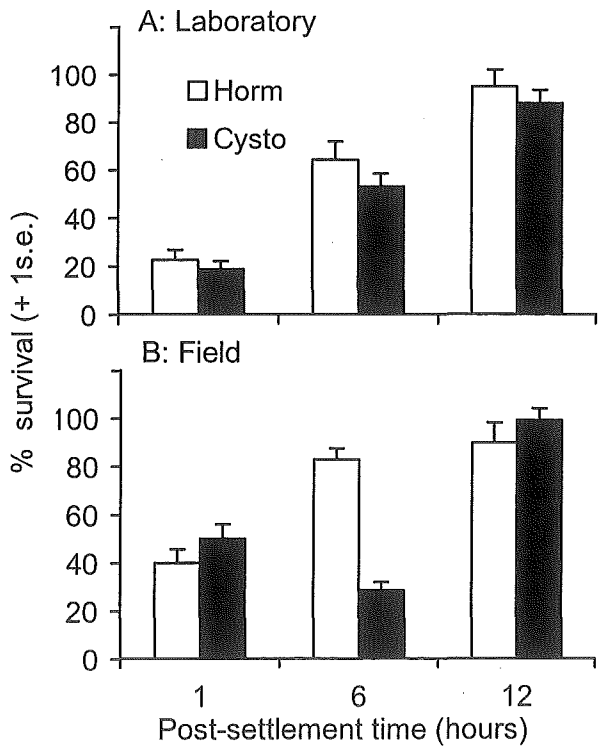

Figure 3.1. The average percent survival of *Hormosira banksii* and *Cystophora torulosa* zygotes when exposed to a single wave in the Laboratory (A) and in the Field (B) when given 1, 6 or 12 hours post-settlement time in the single wave experiments.

Table 3.1 Two factor analysis of variance of the effects of post-settlement attachment time (1, 6 or 12 hours) and species on the percent survival of *Hormosira banksii* and *Cystophora torulosa* after a single wave in the laboratory (A) and in the field (B). Cochran's tests were not significant.

Location	Source	df	MS	F	p
A: *Laboratory*	Settling time	2	22648.39	70.09	0.000***
	Species	1	718.26	2.22	0.143
	Settling time x Species	2	60.19	0.19	0.831
	Residual	48	323.13		
B: *Field*	Settling time	2	12218.79	36.95	0.000***
	Species	1	1822.26	5.51	0.023*
	Settling time x Species	2	6155.46	18.61	0.000***
	Residual	48	330.73		

In the single-wave experiment using *Durvillaea antarctica* and *Hormosira banksii*, there were significant differences in survival between the species and post-settlement times in the laboratory flume (Table 3.2A). For all post-settlement attachment times, *Durvillaea* survived better than *Hormosira* (Fig. 3.2A). *Durvillaea* zygotes had 75 %, 98 % and 99.5 % survival at 1, 6 and 12 hr post-settlement times, while the survival values for *Hormosira* were 2 %, 18 % and 44 %. Although the survival of *Hormosira* zygotes increased as the post-settlement attachment period increased, the survival of zygotes at each post-settlement time was poorer in this experiment than in the earlier comparison with *Cystophora* in the laboratory flume.

Once again, the result was more complicated in the plates exposed to a single wave in the field. There was a significant interaction between species and post-settlement time (Table 3.2B), which was attributable to the similarity in survival of *Hormosira* zygotes in the 6 and 12 hr treatments. As in the laboratory experiment, *Durvillaea* zygotes had much greater survival than *Hormosira* at all post-settlement times. *Durvillaea* survival average 92 % after a 1 hr attachment time, but was almost 100 % at 6 and 12 hr (Fig. 3.2B). As in the laboratory experiment, *Hormosira* had only a few percent of zygotes survive after 1 hr of attachment but this increased to 61 - 65 % at 6 and 12 hr.

Table 3.2. Two factor analysis of variance of the effects of post-settlement attachment time (1, 6 or 12 hours) and species on the percent survival of *Durvillaea antarctica* and *Hormosira banksii* after a single standard wave in the laboratory (A) and in the field (B). Data were unable to be stabilized and Cochran's tests were significant.

Location	Source	df	MS	F	P
A: Laboratory	Settling Time	2	5454.46	21.06	0.000***
	Species	1	66108.99	255.26	0.000***
	Settling time x Species	2	745.60	2.88	0.066
	Residual	48	258.98		
B: Field	Settling Time	2	6958.23	27.76	0.000***
	Species	1	34866.75	139.11	0.000***
	Settling time x Species	2	4082.58	16.29	0.000***
	Residual	48	250.64		

The poorer survival of *Hormosira* during the experiment with *Durvillaea* compared to the experiment with *Cystophora* may be attributable to the experiment being done in winter. This is probably not the optimal reproductive season of *Hormosira* and it may have affected zygote viability or attachment properties. However, all zygotes that survived and remained attached on plates had elongated 24 hours after the experiments, indicating that they were viable. Over the single-wave experiments, there was generally a progression of survival from sheltered to exposed species and from 1 to 12 hours of attachment time (Fig. 3.2C). *Hormosira*, the species most characteristic of sheltered shores, had generally poorer survival than *Cystophora* (found in slightly more exposed situations), which was poorer than *Durvillaea* (found only in exposed conditions). *Durvillaea* clearly exhibited greater 'stickability' than the other species at all attachment times.

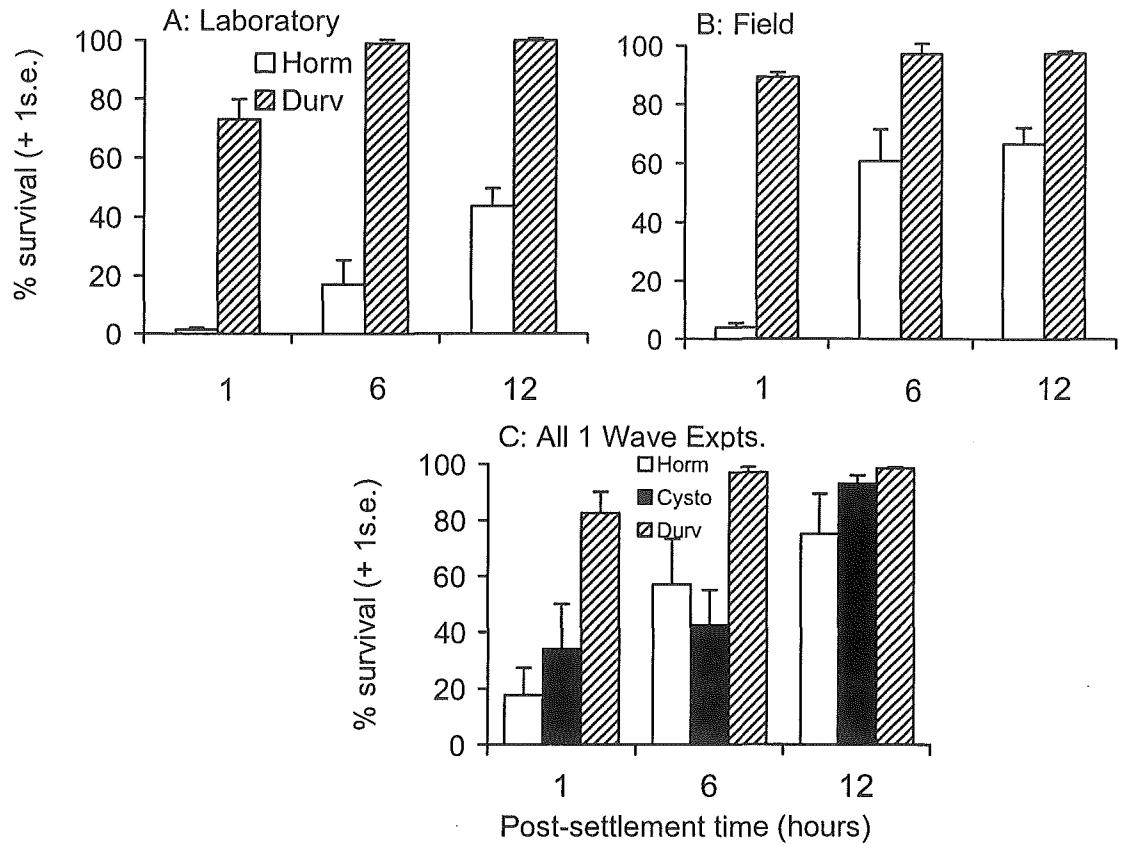

Figure 3.2. The average percent survival of *Durvillaea* and *Hormosira* after exposure to a single wave in the Laboratory (A), in the Field (B) and all species used in all single wave experiments (C) after 1, 6 or 12 hours post-settlement attachment time.

3.3.2 New Zealand full tidal cycle field experiments

When placed into the field for 12 hr at sites within three levels of wave exposure, the effects of settling time on the survival of *Hormosira banksii* zygotes placed in the field varied between sites (Table 3.3A). In all cases, there was far greater survival in the treatments with a 12 hr period of attachment than those attached for 1 or 6 hr (Fig. 3.3A). *Hormosira* zygotes settled for only 1 hr had no greater than a few percent survival in any of the treatments, while those settled for 6 hr averaged no more than 8 % survival. Of the plates settled for 12 hr, the greatest survival (40 %) occurred in one sheltered site, while

the other site within the same exposure had 22 % survival. At the intermediate exposure, survival averaged 22 % and 18 %, while at the exposed sites the averages were 6 and 8 %. For *Hormosira* overall, therefore, there was very poor survival in exposed conditions and only those zygotes with > 6 hr of attachment time remained attached in any numbers after a full tidal cycle.

Table 3.3. Three factor hierarchical model analysis of variance of the effects of exposure (Sheltered, Intermediate and Exposed), sites (random and nested in exposure) and post-settlement attachment time (1, 6, or 12 hours) on the percent survival of (A) *Hormosira banksii* and (B) *Durvillaea antarctica* after 12 hours in the field. Cochran's tests were significant.

Species	Source	df	MS	F	P
A: *Hormosira*	Exposure	2	417.58	7.03	0.074
	Sites (Exp.)	3	59.36	1.94	0.141
	Settling time	2	1483.26	15.02	0.005**
	Exp. x Set. time	4	252.75	2.56	0.146
	Sites (Exp.) x Set. time	6	98.78	3.22	0.012*
	Residual	36	30.66		
B: *Durvillaea*					
	Exposure	2	5423.20	2.12	0.267
	Sites (Exp.)	3	2563.36	11.29	0.000***
	Settling time	2	48.68	0.56	0.600
	Exp. x Set. time	4	110.68	1.27	0.379
	Sites (Exp.) x Set. time	6	87.45	0.39	0.884
	Residual	36	227.128		

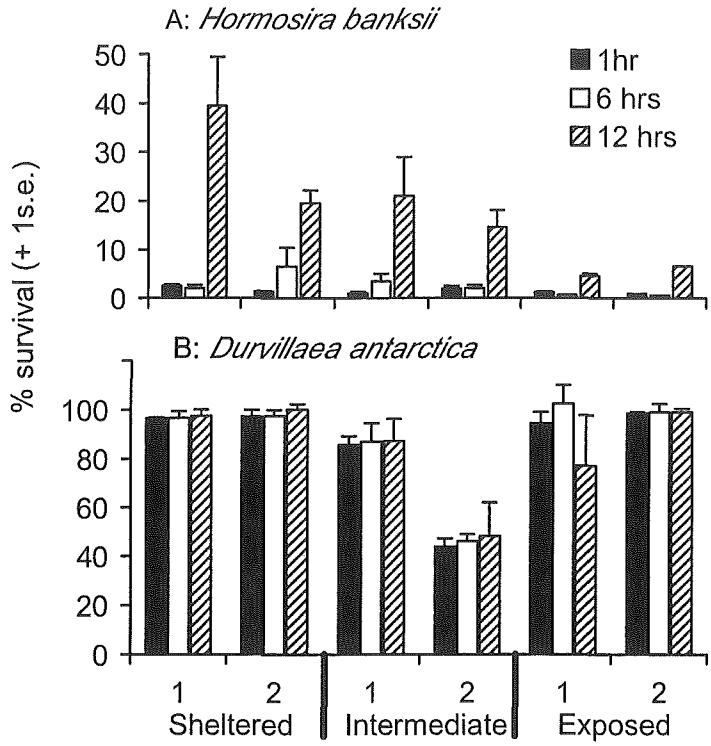

Figure 3.3. The average percent survival of *Hormosira* (A) and *Durvillaea* (B) at sites within three exposures after one tidal cycle and 1, 6, or 12 hours post-settlement attachment time.

The survival of *Durvillaea antarctica* zygotes in the field did not depend on the post-settlement period, but did vary between sites within exposures (Table 3.3B). In most sites within the three levels of exposure, the average survival ranged from 83 - 99.5 % (Fig. 3.3B). The exception was at one of the sites at intermediate exposure, where average survival ranged from 45 -53 %. This site was apparently hit obliquely with some freak waves, but the effect was similar among treatments with different post-settlement times. As in the earlier experiments, therefore, *Durvillaea* zygotes attached quickly and firmly, surviving even after 12 hr in exposed sites subjected to 1.5 m swells.

3.3.3 Oregon full tidal cycle field experiments

Dynamometers showed maximum wave forces were highest at the exposed points of both sites at during all three experiments (Fig. 3.4). In all three Oregon experiments the survival of *Pelvetiopsis limitata* and *Fucus gardneri* zygotes depended on species and post-settlement attachment time but this effect was different between sites. There was no significant difference in zygote survival across exposures in all three experiments.

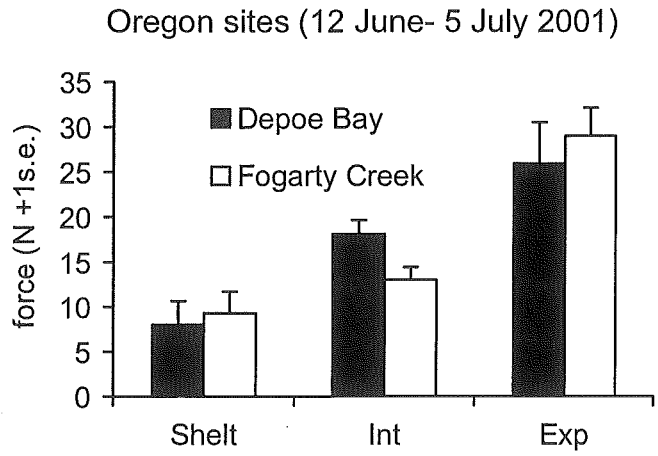

Figure 3.4. Dynamometer data from sheltered, intermediate and exposed sites at Fogarty creek and Depoe bay during the 1999 experiments in Oregon.

Oregon results

The combined results of the three Oregon 'stickability' experiments show that sites and exposures had different magnitudes of effects on each species (Table 3.4). For example, *Fucus gardneri* generally had lower survival across all exposures at Fogarty creek than at Depoe Bay (Fig. 3.5A, B). The same general trend was seen with *Pelvetiopsis limitata* but at the sheltered sites survival was greater at Fogarty Creek (Fig. 3.5C, D). Post-settlement attachment times also had significant effect on surviva (Table 3.4). For example, the survival of *Fucus* given 1 hour of post-settlement attachment time was 18% at the sheltered Depoe Bay site and 6% at Fogarty Creek. When given 6 hours post-

settlement attachment time *Fucus* survival at Depoe Bay ranged from 29% at the sheltered site to 22% at the exposed site (Fig. 3.5A). At Fogarty Creek the 6 hour treatment at the sheltered site had less than c.1% survival while the intermediate site had the greatest survival at c.19% and the exposed site had c.7% (Fig. 3.5B). When given 12 hours post-settlement attachment time both species had survival ranging between 10 and 40% (Fig. 3.5A-D). Overall, there was no significant difference in survival between species across exposures (Table 3.4)

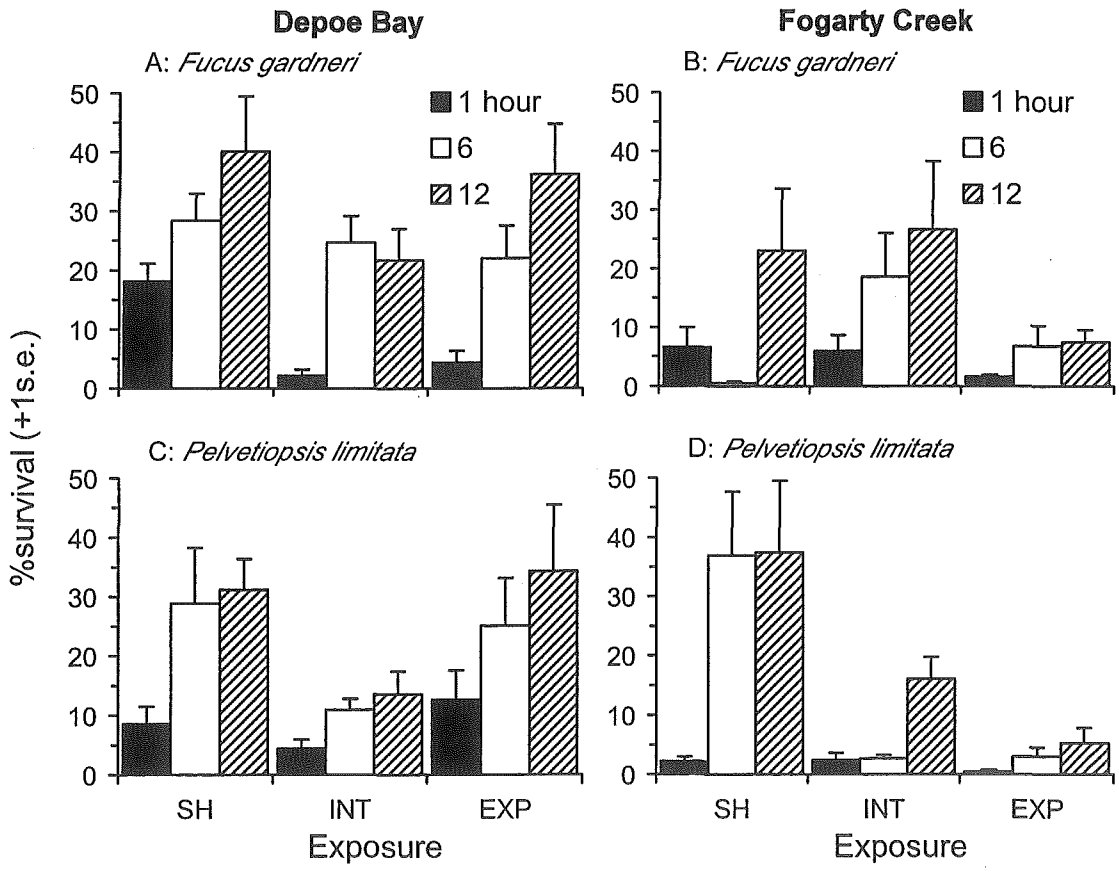

Figure 3.5. The lumped percent survival from the three experiments of *Fucus gardneri* (A, B) and *Pelvetiopsis limitata* (C, D) across three exposures at Depoe Bay and Fogarty Creek after one tidal cycle and 1, 6, or 12 hours post-settlement attachment time.

Table 3.4. Four factor mixed model analysis of variance of the effects of species (*Pelvetiopsis limitata* and *Fucus gardneri*), exposure (Sheltered, Intermediate and Exposed), sites (Depoe Bay and Fogarty Creek, random) and post-settlement attachment time (1, 6 and 12 hours) on percent survival after one tidal cycle in the field in the three Oregon experiments. Data were Arcsin transformed and Cochran's tests were not significant.

Source	df	MS	F	P
Species	1	0.000	0.000	0.992
Exposure	2	0.377	1.662	0.376
Sites	1	0.799	11.587	0.736
Settling time	2	1.065	22.255	**0.043**
Sp. x Exp.	2	0.105	0.601	0.625
Sp. x Sites	1	0.056	0.287	0.637
Exp. x Sites	2	0.227	1.017	0.459
Sp. x Set.	2	0.007	0.176	0.850
Exp. x Set.	4	0.045	0.681	0.641
Sites x Set.	2	0.048	0.543	0.618
Sp. x Exp. x Sites	2	0.174	10.321	**0.026**
Sp. x Exp. x Set.	4	0.105	6.244	0.052
Sp. x Sites x Set.	2	0.039	2.310	0.215
Exp. x Sites x Set.	4	0.066	3.924	0.107
Sp. x Exp. x Sites x Set.	4	0.017	0.436	0.782
Residual	282	0.039		

3.4 Discussion

Life in the turbulent environment of the intertidal zone on temperate shores presents many challenges to resident organisms. Several reviews have discussed the factors affecting the various stages of development of algal stands including gamete release, fertilisation, the dispersal period, settlement, attachment, recruitment and subsequent growth (Chapman, 1985; Santelices, 1990; Clayton, 1992; Fletcher and Callow, 1992; Vadas et al., 1992; Chapman, 1995). The early post-settlement period involves the interaction of microscopic zygotes, embryos and germlings with many physical and biological factors (Amsler et al., 1992). Vadas et al. (1992) list 6 intrinsic factors and 17 extrinsic factors that can influence early post-settlement mortality. Intrinsic factors include properties of species such as germination and spore viability, attachment time, and

growth rates and size. Extrinsic factors include interactions with other species, substratum characteristics and physical environment effects such as temperature and water motion. It has long been recognised, however, that secure attachment is one of the most important events in the life history of intertidal algae (Hardy and Moss, 1979). The New Zealand component of my study focused primarily on water motion and how its effects on the survival of early post-settlement stages varied among three of the most important habitat-forming seaweeds in southern New Zealand. These species have overlapping distributions geographically but not locally. *Hormosira banksii* and *Cystophora torulosa* are both widely distributed species found throughout coastal New Zealand and the offshore islands (Nelson, 1994). Within sites, however, *Cystophora torulosa* is a low-shore species that readily desiccates and dies if emersed for too long. *Hormosira banksii* has a narrow zone of overlap with *C. torulosa* but mostly occurs higher in the intertidal zone and is the most desiccation-resistant of the New Zealand large brown algae (Brown, 1987; Chapman, 1965). Both species are found in sheltered and intermediate conditions of wave exposure and rarely extend into exposed conditions except as isolated and stunted individuals. *Durvillaea antarctica* is found only in exposed conditions and is one of the largest of all intertidal species along parts of the open coast of New Zealand, South America and most of the sub-antarctic islands (Bantham, 1956; Hay, 1979; Nelson, 1994). On a local scale it never extends into sheltered or intermediate conditions. In Oregon, *Fucus gardneri* and *Pelvetiopsis limitata* are two of the most common fucoid algae on intertidal platforms in Oregon (Ricketts et al., 1969; Kim, 1997). Both species are most abundant at intermediate and sheltered sites but can be found as small plants in wave exposed situations, often recruiting onto barnacle tests in the upper tidal zones (Cubit, 1984; Kim, 1997; Blanchette, 1999). A few plants of *Fucus gardneri* were observed in the lower tidal zone at Fogarty Creek but neither species are abundant in the lower tidal zones on exposed shores.

The results of the New Zealand 'stickability' study indicate that the ability to remain attached immediately after settlement represents a major bottleneck in the establishment of at least two of these species across wave exposures. Attachment ability

broadly correlated with the natural distribution of these species across a wave exposure gradient with overall rankings of average survival of *Durvillaea* > *Cystophora* > *Hormosira*. Furthermore, both *Hormosira* and *Cystophora* required at least 6 hr to adhere to surfaces, even in sheltered conditions, while *Durvillaea* adhered well and quickly in all experimental conditions. It is a tautology to say that theses are well adapted in their early stages to the environment in which they normally occur. However, there are clear and important differences in the propagules of each species.

Most algal propagules sink slowly through water, which is a viscous medium to objects only 50-100 μm in diameter (Amsler et al. 1992; Norton, 1992). Both *Cystophora* and *Hormosira* have relatively large propagules (60-120μm) that sink slowly, which is typical of fucalean algae (Clayton, 1992). *Durvillaea antarctica*, however, releases very small propagules (30μm) in packets of four that are relatively buoyant, probably because of small size and the copious amounts of mucilage released simultaneously (Clayton, 1992), and can remain suspended for up to 15 minutes in calm test-tube conditions (Taylor, unpublished data). The differences among species in size and buoyancy clearly signal that their pre-settlement processes and adaptations are likely to be quite different.

Gamete release in *Hormosira banksii* and *Cystophora torulosa* occurs at low tide in calm conditions, although it is not known if this is exclusively so. This is typical of fucalean species. For example, gamete release in *Fucus distichus* occurs during low tides in periods of very low water motion (Pearson and Brawley, 1996). High water motion can inhibit gamete release in *F. versiculosus*, *F. distichus* and *Pelvetia fastigiata* and result in low fertilisation success (Serrao et al., 1996). Release of gametes during low-tide on calm days into tide pools and shallow concavities on reefs allows several hours for attachment to the substratum to occur. The processes following gamete release in *Hormosira* and *Cystophora torulosa* are similar to most fucaleans (Fletcher and Callow, 1992; Clayton 1992). Two or three hours after fertilisation *Hormosira* zygotes become sticky from extracellular mucilage and adhere to the substratum (Forbes and Hallam, 1979). At 5 hours, a gentle jet of water will not dislodge them and at 8 hours they appear to be firmly attached. Not

until 16 hr after fertilisation have 50% of zygotes developed rhizoids. In other species of fucaleans, there are two periods of greater mortality at these very early post-settlement stages. The first is immediately after settlement, before sufficient mucilage is produced for adhesion, and the second is just after the rhizoids have formed and the mucilage attachment weakens at 24-48 hours (Brawley and Johnson, 1991). The 'stickabilty' experiments extended only through the period of attachment by mucilage. For both *Hormosira* and *Cystophora torulosa*, the attachment was strongest at 12hr, a period that exceeds the emersion time at low tide. Across exposures, *Hormosira* had no more than 8% survival and this was only at the calmest sites. The better adhesion at 12 hr after settlement strongly implies that successful attachment is likely to occur only in the calmest conditions, which rarely, if ever, take place at exposed sites.

In contrast, *Durvillaea antarctica* zygotes attach immediately and firmly to almost any surface. Even wiping a gamete-releasing frond over a surface results in extensive attachment of zygotes by a sticky mucilage. In all 'stickability' experiments, adhesion of zygotes was almost 100% in most cases and did not depend on the degree of exposure to water motion. The processes and timing of gamete release, dispersal ability and settlement are not clear in this species. Adult plants occur in the low-shore at the subtidal boundary and are rarely exposed entirely except during the lowest tides. Release has been observed at low tide in calm conditions but it is known if this is exclusively so (Taylor pers. Obs.). Two processes of attachment can be hypothesised. Because oogonia are released in packets of four within copious quantities of dense mucilage they probably remain near the surface and are propelled quickly shore-wards at low tide where they are likely to contact substrata near adult plants. The other means of short-range dispersal is by gamete-releasing fronds coming into direct contact with the shore. *Durvillaea* "smears" of gamete-bearing mucilage have been observed on bare rock at low tide, but the frequency of this occurrence is unknown. However, because propagules of *Durvillaea* are relatively buoyant this species clearly has a potential mechanism for medium to long-range dispersal of propagules in comparison to other intertidal fucoid algae. Even though the non-floating

propagules of intertidal fucoids are likely to be suspended in the turbulence of water motion nearshore for short periods (Norton, 1992), they do not seem to be able to attach quickly and securely, therefore they probably have little ability to disperse effectively as propagules. For *Durvillaea antarctica*, however, the ability of propagules to adhere quickly and securely may make relatively long-range dispersal effective. The inshore area around southern New Zealand reefs can be strongly influenced by along-shore transport (Chiswell and Schiel, 2001), which provides a potential avenue of dispersal of along the coast.

The results of the Oregon experiments indicate that the period immediately after settlement represents a major bottleneck in the establishment of *Fucus gardneri* and *Pelvetiopsis limitata* across wave exposures. In general, both species required around 6 hours post-settlement attachment time for secure attachment. Brawley et al.(1976) found similar results in laboratory studies on *Fucus*. They showed that in calm laboratory conditions firm attachment of *Fucus* zygotes occurs at 4-6hrs after fertilization as the abundance of sulphated fucans around zygotes increases. These results have important implications for the abundance of these species across wave exposures and suggests that successful settlement of these species in the lower tidal zones on exposed situations would only occur on calm days during lower tidal cycles. *Fucus gardneri* is most abundant in more sheltered areas and I expected attachment time to limit survival at exposed sites. However, while this trend was evident at Fogarty Creek, wave exposure did not have a consistent effect on survival of *Fucus* or *Pelvetiopsis* because of large between site variation.

Experiments in Oregon were done during extreme low tides, during which, the upper tidal zone was regularly emersed for periods of up to 12 hours. During these low tides mature plants of both species were observed releasing gametes, but gamete release also occurs during calm periods of immersion (Pearson et al., 1998; Brawely et al., 1999). Several species of *Fucus* are know to release gametes at low tide (Brawley et al., 1999). However, results from their earlier study show that if released during low tide periods the chance of fucoid zygotes surviving is reduced due to desiccation stress (Brawley and

Johnson, 1991). The survival of zygotes released at low tide is, therefore, dependent on the microhabitat into which they are released.

Many factors affect the viability of settled algal propagules. Substratum characteristics such as surface heterogeneity, texture of microsites and ability to retain water can affect early survival (Harlin and Linbergh, 1977; Hardy and Moss, 1979; Brawley and Johnson, 1991,1993). One problem in assessing processes across different wave climates is the non-orthogenality of rock-types across different levels of exposure. Softer sedimentary rock-types such as sandstone and siltstone often support very different algal communities to harder metamorphic and volcanic rock surfaces such as marble and basalt (Hartog, 1968; Stephenson and Stephenson, 1972; Fletcher and Callow, 1992). In southern New Zealand and Oregon, intertidal platforms at exposed sites are often composed of harder volcanic or metamorphic rock while reefs at many sheltered sites are composed of softer rock types like mudstone and sandstone. Rock type was not a factor in these experiments because standard plates were used, that are known to be good surfaces for algae to survive and grow on across exposures. Although the role of rock type in determining algal community development is largely unknown, it could be an important factor in the failure of large species such as *Durvillaea antarctica* to extend into more sheltered shores, even if they successfully settled there. As the size of developing plants increases, the forces exerted by waves may exceed the strength of attachment (Vogel, 1984; Denny, 1995). This may not necessarily be due to the attachment strength of the holdfast to the substratum but because the substratum itself fractures so easily. For example, it is not uncommon to see *Durvillaea* detached and cast up on the beach still firmly attached to a piece of fractured rock. Rock type could also indirectly affect algal distribution by controlling the abundance of organisms on which propagules settle. For example, barnacles are often restricted to hard rock platforms and several studies have shown that the recruitment of *Fucus gardneri* and *Pelvetiopsis limitata* is highly dependent on substratum heterogeneity and the presence of barnacle tests that provide protection from invertebrate grazers and desiccation stress (Cubit, 1984; Kim, 1997).

My New Zealand experiments clearly highlight the differences between species in their initial post-settlement period. In New Zealand, the lack of intrusion of the more sheltered species, *Hormosira banksii* and *Cystophora torulosa*, into exposed situations seems greatly influenced by their inability to attach securely. Moreover, because reproductive stands of these species in exposed areas are small and confined to cracks, whatever gamete arrival, attachment and settlement that occurs is likely to be in low numbers. This may affect fertilisation success (e.g. Denny and Shibata, 1989; Reed, 1990(b); Serrao et al., 1996; Brawley et al., 1999) and potentially other factors that are density dependent. Low-density settlement may also provide too few numbers to survive other processes such as grazing, competition and desiccation (Reed, 1990; Vadas et al., 1992; Worm and Chapman, 1996; Kim, 1997; Worm and Chapman, 1998).

The viability of settled zygotes may also be different among species and across environmental gradients. For the species we examined there appear to be narrow windows through the bottleneck for securing a place on a reef. *Hormosira banksii* and *Cystophora torulosa* need extended calm periods to attach successfully but these must also coincide with times when they will not desiccate (c.f. Brawley and Johnson, 1993; Underwood, 1998). For *Durvillaea antarctica*, the reproductive period is relatively brief and occurs during the stormy winter months when turbulent conditions prevail. Although it is capable of remaining attached in all conditions, its absence from more sheltered areas suggests other processes are determining its distribution. For example, fertilised zygotes may simply not arrive in sufficient numbers to establish on shores outside its adult range (Clayton, 1990; Reed et al., 2000). For *Fucus gardneri* and *Pelvetiopsis limitata* the processes determining their distribution across exposure gradients are more complicated and may relate to factors like dispersal distance, the effects of grazing invertebrates and the presence of barnacle tests that provide a refuge from grazers, desiccation and wave stress.

Chapter 4

EARLY POST-SETTLEMENT STAGES OF HABITAT-FORMING ALGAE ACROSS EXPOSURES:

Hemispheric comparisons of grazing and growth-rate

4.1 Introduction

The processes affecting the survival of microscopic algal life stages between settlement and successful recruitment to visible size are not straightforward. High mortality is a common feature of algal populations between settlement and recruitment (Santelices, 1990; Chapman, 1995). Vadas et al. (1992) list 6 intrinsic variables, such as growth rate and attachment strength, and 17 extrinsic variables such as grazing, desiccation and competition that are known to influence the post-settlement survival and growth of early life-stages of algae. The combined effects of these variables can be significant and cause differences between settlement and recruitment patterns (Reed et al., 1988; Reed, 1990a, b). For most algal species the proportion of settled propagules that reach recruit stage is very low. For example, Schiel (1981) found the number of *Sargassum sinclairii* reaching visible recruit stage was less than 5% of those that settled. Ang (1991a) found similar results for *Fucus distichus* in which between 0.4-12% of settlers reached recruit size. These are considerably higher survival rates than those found for kelps where rates between 0.0002 -0.00001% have been observed (Chapman, 1984a, b, 1985). Consequently, survival through the early post-settlement stages represents a bottleneck for many algal populations (Schiel and Choat, 1980; Lubchenco, 1983; Santelicies, 1990; Brawley and Johnson, 1991; Vadas et al. 1990, 1992).

Because of their microscopic size, the early life stages of algae are dominated by viscous forces in a heterogenous chemical, physical and biological microenvironment

(Reed, 2000). In their review, Amsler et al. (1992) described the complex microhabitat of early life stages of macroalgae. Once attached to the substratum they become part of a thin layer of water near the bottom called the benthic boundary layer. The chemical and biological properties of the boundary layer are often distinct from the water above because of secretory activities of microfilm organisms and nutrients, and possibly toxins, produced by bacteria and other micro-organisms. The benthic boundary layer is also the domain of micrograzers and a source of food for larger invertebrate grazers that can have significant effects on the growth, structure and diversity of algal communities (eg. Lubchenco, 1980; Schiel 1981; Underwood, 1980; Brawley and Adey, 1981a, b; Hawkins 1983; Dayton et al., 1984).

The depth of the benthic boundary layer is affected by water velocity and associated turbulence in the water column above (Vogel, 1981, 1984). Also affected by water velocity and turbulence in the intertidal environment are the organisms living above the benthic boundary layer. Several models of intertidal community structure assume or predict that grazer efficiency and grazer effects will be greatest in benign environments and that grazing will be less important or effective in harsh environments (eg. Menge and Sutherland, 1976, 1987). However, despite the apparent importance of grazers in many studies of algal communities, interpretation of results is often complicated by the sizes of algae used (Underwood, 1980; Hawkins and Hartnoll, 1983; Santelicies, 1990; Vadas et al. 1992), the growth rates of algae (Underwood and Jernakoff, 1981; Lotze et al. 2001), grazer preferences (Chapman and Johnson, 1990; Lotze et al., 2000) and variations in grazer abundance (Black, 1976; Lubchenco, 1978, 1983; Petraitis 1987, Menge et al. 1993; Underwood, 1998; Lotze and Worm, 2000). Consequently, grazers can have variable effects on algal communities. For example, Chapman (1989) found no effect of grazers on the recruitment of juvenile *Fucus spiralis*. Foster (1982) found grazers had little effect on *Iridaea* populations, while Chapman and Johnson (1990) found grazers had a significant effect on the survival of transplanted juveniles of *Fucus distichus* in Nova Scotia. In a more recent example, Lotze and Worm (2000) found grazer

importance to be life-stage specific and species-specific, with grazers preferring early life stages of *Enteromorpha* species over *Pilayella littoralis* at all life stages but these effects varied with the species and type of invertebrate grazer. Grazers can also enhance algal recruitment. For example, Dayton et al. (1984) suggested that herbivores holding algal fronds near the substrate may increase settlement and recruitment. Furthermore, several studies have found grazers can speed up succession and increase recruitment of perennial algal species by removing ephemeral species (e.g., Lubchenco, 1978; 1983; Kim, 1997).

The length of time early life stages remain in the benthic boundary layer is determined by their growth-rate. Differences in biomass and growth rates of older life-stages of algae across gradients of wave exposure have been found. For example, Sjøtun et al. (1998) found that the biomass and growth of 4-year-old *Laminaria hyperborea* in Norway showed a positive relationship with wave exposure. In contrast, Gerard and Mann (1978) found that the production of *Laminaria saccharina* was greater at a wave-sheltered site than at a wave exposed site in Nova Scotia. Possible causes of these differences in growth rates may relate to turbulence across blade surfaces and the transfer of nutrients across the blade boundary layer. Hurd et al. (1996) examined the effects of blade microtopography on nutrient uptake for adult stages of macroalgae and found turbulence increased with blade surface heterogeneity but also found highly variable growth rates. For microscopic algal stages, however, the blade surface heterogeneity is probably less important than the microtopography of the surrounding habitat (Brawley and Johnson, 1991). The growth of microalgae is influenced by light and nutrients, which in turn affect interactions with biological variables like grazers and competition within and between species (Underwood, 1985). The quality and quantity of light and nutrients in the microbenthos is highly variable and determined by microhabitat differences that can lead to large differences in survival and growth rates of algae at micro-scales (Brawley and Johnson, 1991; Amsler et al., 1992). For example, in several German studies, the addition of nutrients resulted in different community structure because growth rates of early life-stages of macroalgae differed between species (Lotze and Worm, 2000; Lotze et

al., 2000, 2001). The question of whether growth rates of fucoid algae at microscopic stages vary across wave exposure gradients has not been addressed.

There are clear differences in the dominant habitat-forming algae across exposures on the intertidal platforms of the eastern coast of southern New Zealand (Morton and Miller, 1968; Schiel and Taylor, in prep.). In wave-exposed situations, the dominant alga is the large bull kelp *Durvillaea antarctica* (Chamisso) Hariot (Family Durvillaeales), the biomass of which can reach 80 kg per m^2. However, the distribution of *Durvillaea* does not extend to more sheltered shores, which instead are dominated by fucalean algae such as *Cystophora torulosa* (R. Brown) J. Agardh on the lower shore and *Hormosira banksii* (Turner) Descaisne on the mid shore. With the exception of small plants in cracks and tide pools (Osborn, 1948), *H. banksii* is not found in wave-exposed situations. While there are clear differences in the abilities of propagules of these species to attach quickly to the substratum, this alone does not preclude them from settling in areas of higher and lower wave exposure levels (Taylor and Schiel, In Press). For example, as mentioned in the previous chapter, 'stickability' does not explain the absence of *Durvillaea antarctica* from more sheltered situations.

On intertidal platforms along the exposed Oregon coast and further north fucoid algae are largely constrained to the upper tidal zones in and around barnacle habitat (Cubit, 1984; Blanchette, 1997; Kim, 1997). The most abundant species of fucoid algae are *Pelvetiopsis limitata* and *Fucus gardneri* (Abbott and Hollenberg, 1976). *F. gardneri* is most abundant in the mid tidal zone in sheltered conditions but also survives in the high shore at exposed sites in a smaller morphological form (Blanchette, 1997). *P. limitata* is abundant only in the high tidal zone and is most common in more exposed situations. Associated with *P. limitata* and *F. gardneri* habitats are large numbers of small invertebrate grazers, particularly limpets like *Lottia digitalis, L. strigatella* and *L. pelta* that can reach up to 400 per $0.25m^2$ (Cubit, 1984; Pers. obs.).

An understanding of whether similar processes, like grazing, are determining similar patterns of habitat-forming algae across intertidal gradients over large spatial scales

remains a major goal in marine ecology (Lubchenco, 1983; Underwood, 1980; Hawkins and Hartnoll, 1983; Johnson et al., 1997; Menge et al., 1999). The Oregon intertidal system provides an interesting contrast to New Zealand because they are at a similar latitudes in the northern and southern hemispheres and consequently are subject to broadly similar environmental conditions (Menge et al., 1999). My study tests the relative importance of grazing in determining the survival of fucoid algae across wave exposures in the lower tidal zone on intertidal shores in New Zealand and Oregon.

This chapter examines the degree to which the observed patterns of distribution and abundance of habitat-forming large brown algae are related to the ability of their early post-settlement stages to grow and survive in the biological and environmental conditions associated with different levels of wave action. Furthermore, my experiments specifically test predictions of community models like the 'Environmental Stress Model' proposed by Menge and Sutherland (1987) that the relative effects of invertebrate grazers in determining community structure will be greater in benign environments.

In this chapter I test two null hypotheses: 1) the early post-settlement stages of *Durvillaea antarctica*, *Hormosira banksii* in New Zealand and *Fucus gardneri* and *Pelvetiopsis limitata* in Oregon will grow and survive equally well across wave exposures; 2) the effects of invertebrate grazers on germling survival are the same across wave exposure gradients. I test these hypotheses in the northern and southern hemispheres across local scale wave exposure gradients (for *Hormosira, Durvillaea, Fucus* and *Pelvetiopsis*) and at regional scale wave exposures gradients (for *Hormosira* and *Durvillaea*). For *Durvillaea antarctica* and *Hormosira banksii* I test these hypotheses at regional scales on two occasions.

4.2 Materials and methods

I did two sets of experiments (Table 4.1). The regional-scale transplant (RT) experiments were done at sites of different wave exposures separated by up to 100km. These tested the effects of wave exposure on algal germlings on a broad spatial scale. The local-scale transplants (LT), were done at areas of different wave exposures within sites, testing the smaller scale influences of biological and physical factors associated with wave exposures and enabled finer temporal scale sampling. In all experiments, I refer to "survival" as the average number of germlings per cm^2 remaining over time in relation to the initial mean per cm^2 for each plate at the beginning of the experiment.

Table 4.1. The timing of regional and local scale transplant experiments using early life stages of habitat-forming algae across wave exposure gradients in New Zealand and Oregon. Experiments tested the null-hypotheses that: 1) survival and growth of algae are the same across exposures; 2) the importance of invertebrate herbivores in determining the survival of algae is the same across exposures and across hemispheres.

Hemisphere	*Species*	*Regional-scale Experiments*(RT)	*Dates*	*Local-scale Experiments* (LT)	*Season started*
Southern (New Zealand)	*Durvillaea antarctica*	Yes (n= 2)	May - July 1999; 30th July 1999 - Nov. 2000	Yes	Winter 2001
	Hormosira banksii	Yes (n= 2)	March - April 1999; June – Nov. 1999	Yes	Late Summer/ Autumn 2002
Northern (Oregon)	*Fucus gardneri*	No		Yes	Summer 2001
	Pelvetiopsis limitata	No		Yes	Spring 2002

4.2.1. Study sites

For the regional transplant experiments germlings were settled at the Edward Percival field station in Kaikoura (42°25'S, 173°41'E). The RT experiments were done at two sites within each of three categories of wave exposure around Kaikoura and Banks peninsulas. These locations have sites of a wide range of exposures to wave action, from

sheltered sites in the lee of headlands protected from oceanic swells, to very exposed sites continuously exposed to oceanic swells. The wave exposure categories were Sheltered, Intermediate and Exposed. They were selected on a visual basis initially but were also verified using dynamometers (Bell and Denny, 1994), during experiments (Fig. 4.23). Sheltered sites were Mudstone Bay at Kaikoura and Devauchelles Point at Banks Peninsula. Intermediate sites were Seal Point Carpark (Kaikoura) and Caves Bay (Banks Peninsula). The exposed sites were Raramai Point (Kaikoura) and Boulder Bay Point Banks Peninsula. The RT experiments were done twice allowing a comparison of growth rates within each species at different times (see below).

During the second set of RT experiments a thermistor was installed at each site, which logged the temperature in the low shore of all sites for the duration of the experiments. However, the thermistor at the Caves Bay site was stolen.

The local transplant experiments were done at Seal Reef and First Bay on the eastern side of Kaikoura Peninsula in New Zealand and, for comparison, methodologically identical experiments were done at Depoe Bay and Fogarty Creek on the Oregon coast (see Chapter 1, Fig. 1.5). Within these locations, sites representing three levels of wave exposure were selected and dynamometers (Bell and Denny, 1994) were used to verify these selections (Fig. 4.24). LT experiments were done during New Zealand spring-summer 2001/2002 using *Durvillaea antarctica* and autumn 2002 using *Hormosira banksii* and in the US summer 2001 using *Fucus gardneri* and in spring 2002 using *Pelvetiopsis limitata* (see below).

All experiments were done in the lower tidal zones (approximately 0.3m above chart datum) of each site. Algal canopies were removed from the area around experiments at all sites so that they would not interfere with experiments. Plate areas were chipped-out from the substratum using a masonry hammer to ensure that plates sat flush with the reef. Before and during experiments, five 0.25m^2 quadrats were haphazardly placed around the experimental areas and the number of invertebrate grazers was monitored.

To account for concealed species the number of invertebrate grazers in five 1m long cracks was also monitored .

4.2.2. Species studied

Experiments using different species were done at different times (Table 4.1), dictated by the reproductive periodicity of species, weather conditions and accessibility . *Durvillaea antarctica* is a dioecious species that releases gametes naturally over about a 16 week period during austral winter (May –August) (Hay, 1979b; Clayton, 1990; Pers. obs.). Raised male and female conceptacles scattered over the blades identify reproductive plants (Adams, 1994). *Hormosira banksii* is a perennial, dioecious, fucalean alga that dominates the middle to lower shore on many sheltered and intermediately exposed platforms. Populations release gametes throughout the year, but there are large pulses of release during the warmer months (September - April) (Schiel unpublished data). *Fucus gardneri* and *Pelvetiopsis limitata* are perennial, monoecious fucoid algae that are reproductive year-round but have reproductive peaks during the northern autumn and winter (Ang, 1991). There is no obligate planktonic developmental stage for any of these species.

During austral winter of 2000 and 2001 (for *Durvillaea antarctica* and *Hormosira banksii* experiments), austral spring and summer 1999 / 2000 (for *Hormosira* RT experiments), and boreal summer 2001 (*Fucus gardneri*) and boreal spring 2002 (*Pelvetiopsis limitata*) reproductive male and female plants were collected in the field and returned to the laboratory where they were refrigerated at 4°C for 24 hours. Exposing plants to sunlight and warmth initiated gamete release. Gametes were washed from the adult plants using seawater, concentrated in glass beakers and left to allow fertilisation. The zygote suspension was then poured gently over plates covered with 1cm of seawater. Approximately 100 plates were seeded for each experiment in large plastic trays.

4.2.3. Experimental Design

Fibre-based cement plates were used as a standard synthetic substratum for settlement. They have been used in numerous experiments and are good surfaces for retaining water and for algal attachment. Plates were 7 mm thick and 11cm x 11cm. They were soaked in seawater for 24 hours before settling with zygotes to ensure plates were equally saturated with water. Seeded plates were kept in running seawater for around 4 days before transplanting. Before and during each experiment, the number of germlings on each plate was estimated by viewing the damp plate beneath a dissecting microscope and counting five random 1 cm^2 quadrats. For the New Zealand species I aimed for a settlement density of 500-1000 cm^{-2}. Five bare settlement plates placed under canopies of *Durvillaea antarctica* and *Hormosira banksii* for 1 week during peak reproductive season showed this was comparable to natural settlement densities on five plates (Fig. 4.1). Settlement densities up to 3000 cm^{-2} have been recorded for these species (Schiel and Dunmore, in progress). For the Oregon species, settlement densities were between 100 - 300 cm^{-2}, reflecting lower natural settlement densities found on plates under natural canopies (Pers. Obs.). Percent survival was calculated as the average number of germlings remaining attached on each plate. Growth was estimated from 10 random germling lengths per plate using a microscope graticule.

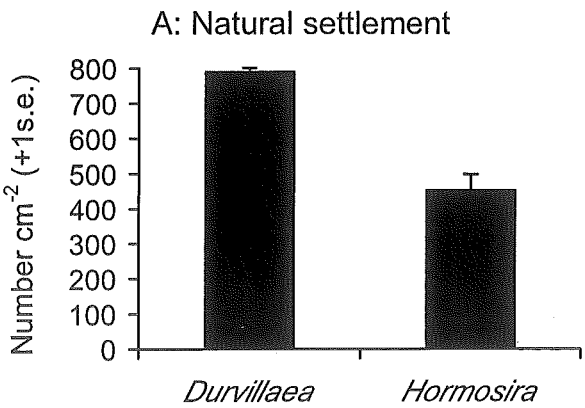

Figure 4.1. Natural settlement of *Durvillaea antarctica* and *Hormosira banksii* on fibre plates under adult canopies during peak reproductive season in 1999.

The RT experiments, done twice, tested the relative ability of germlings of *Hormosira banksii* and *Durvillaea antarctica* to grow and survive across a wave exposure gradient. *H. banksii* experiments were done from March - April 1999 and from June - Nov 1999. *D. antarctica* RT experiments were done from May - July 1999 and from July 1999 - Nov 2000. Plates were randomly assigned within three treatments: "fence" to test the effect of invertebrate grazer exclusion; "fence control", which had holes to allow access to grazers, testing effects of the fence; "open" plates tested the effects of grazers in the absence of a fence. Fences consisted of 5cm high stainless steel mesh with a 2cm overhanging lip. Fence controls were of the same construction but had 2x3cm holes cut in two sides to allow access to invertebrate grazers. Open plates had no fence. Plates were taken to the shore, randomly assigned to four replicates of each treatment and positioned randomly at each site at least 20cm apart to ensure independence. A single 8mm hole was drilled into the rock for each plate into which was placed a plastic rawl plug (Ramset 8mm). Plates were attached using a single 8mm stainless steel screw and washer (15mm diameter) through the middle of the plate. Plates were removed from the rock and germlings were counted in the field using a dissecting microscope set up on the shore. The number of germlings remaining on each plate was estimated from counts in five random 1cm^2 areas of each plate. I tried to monitor plates at similar intervals in each experiment but weather conditions dictated exact monitoring dates.

To control for the effect of handling plates and transferring them to treatments, initially three seeded control plates for each species were taken to the field and then returned to the laboratory. All of these control plates had 100% survival.

To estimate the percent of mortality attributable to grazing, the percent of germlings lost in fenced treatments was subtracted from the percent lost in fence control treatments. Furthermore, by subtracting the percent of germlings lost on the fence control from the open plate treatments a measure of the 'fence effect' was calculated. This assumed that the fence control treatment had no effect on the behaviour or aggregation of grazing invertebrates. No such effects were seen. I adjusted the percent lost to grazing

by subtracting the 'fence effect' from the 'grazing effect'. In doing so I reduced the chance of overestimating the importance of grazing. Negative values represent a 'fence effect' from either greater survival on open plates than in fence treatments, or greater survival on fence control plates than on open plates.

Analysis of variance tests (ANOVA) were used to analyse for treatment effects on percent survival of germlings at each monitoring date and to compare grazer abundance across exposures in cracks and on flat rock. The model treated 'Sites' as a random factor. All data were tested for homogeneity of variances using Cochran's test prior to ANOVA. Percent cover data were arcsine-transformed and grazer abundance data were log-transformed prior to analysis. In most cases, these tests were non-significant unless otherwise stated. In some cases (see Results) the variances could not be equalised, so results should be cautiously interpreted (c.f., Underwood, 1997). Analyses were done using the General Linear Model package in Statistica 6.0 (Statsoft Inc.).

4.3 Results

4.3.1 Regional-scale Transplant experiments

4.3.1.1 Hormosira regional transplant #1

In the *Hormosira banksii* RT experiment begun in February 1999 the fence treatments excluding invertebrate grazers had greatest survival (Fig. 4.2A-F). After 11 days in the field, survival of germlings neither exposure, site or treatment had significant effects on survival (Table 4.2). At 25 days there was a significant interaction between exposures, sites and treatments (Table 4.2). At this time, plants protected from grazers at the sheltered Kaikoura site had around 30 % survival compared to the 2 % survival at the sheltered Banks Peninsula site (Fig. 4.2 A,D). The fence controls at the intermediate Kaikoura site also had greater survival than the equivalent treatment at Banks Peninsula. At Day 56 there were no significant treatment effects (Table 4.2). However, survival in the fenced treatment at the sheltered Kaikoura site remained high (7%) compared to all other treatments which related to around 3500 plants per plate.

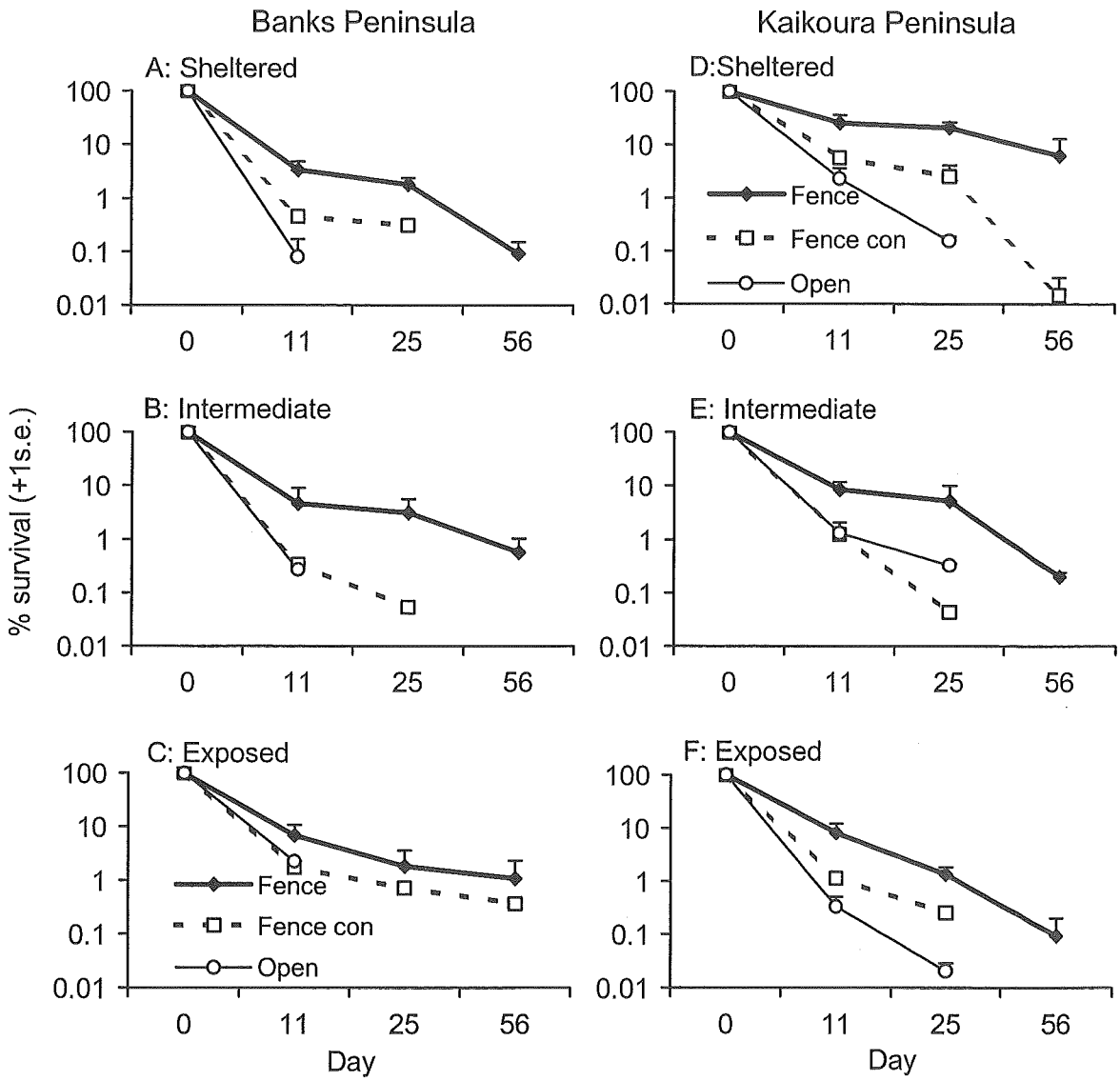

Figure 4.2. Percent survival of *Hormosira banksii* germlings over time transplanted across a regional wave exposure gradient from February - April 1999 on Banks Peninsula (A-C) and Kaikoura Peninsula (B-F).

Table 4.2. ANOVA results of survival of *Hormosira banksii* germlings transplanted across a regional wave exposure gradient in February 1999 over time. Sites were treated as random. Day 11 data were square root arcsine transformed to equalize variances. Cochran's tests were significant at all other times and results were not considered significant unless $p \leq 0.01$.

	Day 11				*Day 25*		
Factor	df	MS	F-ratio	p	MS	F-ratio	p
Exposure	2	0.009	0.491	0.671	86.178	0.887	0.530
Site	1	0.027	1.046	0.396	117.741	1.010	0.454
Treatment	2	0.054	3.954	0.202	228.576	2.680	0.272
Exp x Site	2	0.018	3.016	0.159	97.202	1.474	0.331
Exp x Trt	4	0.004	0.691	0.635	61.291	0.929	0.527
Site x Trt	2	0.014	2.236	0.223	85.291	1.293	0.369
Exp x Site X Trt	4	0.006	1.895	0.125	65.955	5.627	0.000*
Error	54	0.003			11.722		

	Day 56			
Factor	df	MS	F-ratio	p
Exposure	2	6.316	0.553	0.644
Site	1	4.579	0.679	0.672
Treatment	2	14.882	2.602	0.278
Exp x Site	2	11.416	1.098	0.417
Exp x Trt	4	6.856	0.659	0.652
Site x Trt	2	5.721	0.550	0.615
Exp x Site X Trt	4	10.396	1.269	0.294
Error	54	8.195		

4.3.1.2 Durvillaea antarctica regional transplant #1

The results of the first *Durvillaea antarctica* RT experiment, begun in May 1999, were similar to those of the first *Hormosira* experiment. Survival rates in the fence treatments were consistently higher across exposures. After 7 days there was no difference in survival of *Durvillaea antarctica* germlings across exposures but survival between treatments did vary significantly (Table 4.3). This was because survival on open and fence control treatments across exposures at day 7 was less than 1 percent at all but the sheltered Kaikoura site where they had 9 percent (Fig.4.3A). Fenced treatments that reduced invertebrate grazing had only around 7 percent survival, which translated to c. 3500 plants per plate across exposures. Similar patterns in survival were found after 20 days in the field. After 60 days there were low numbers of *Durvillaea* germlings in all

fence treatments but variability was high and the interaction effect between Sites and treatment was not significant (Fig. 4.3A-F; Table 4.3). At day 60 there were c.750 germlings per plate in fence treatments at exposed and sheltered sites but less than 70 per plate at the intermediate Banks Peninsula site.

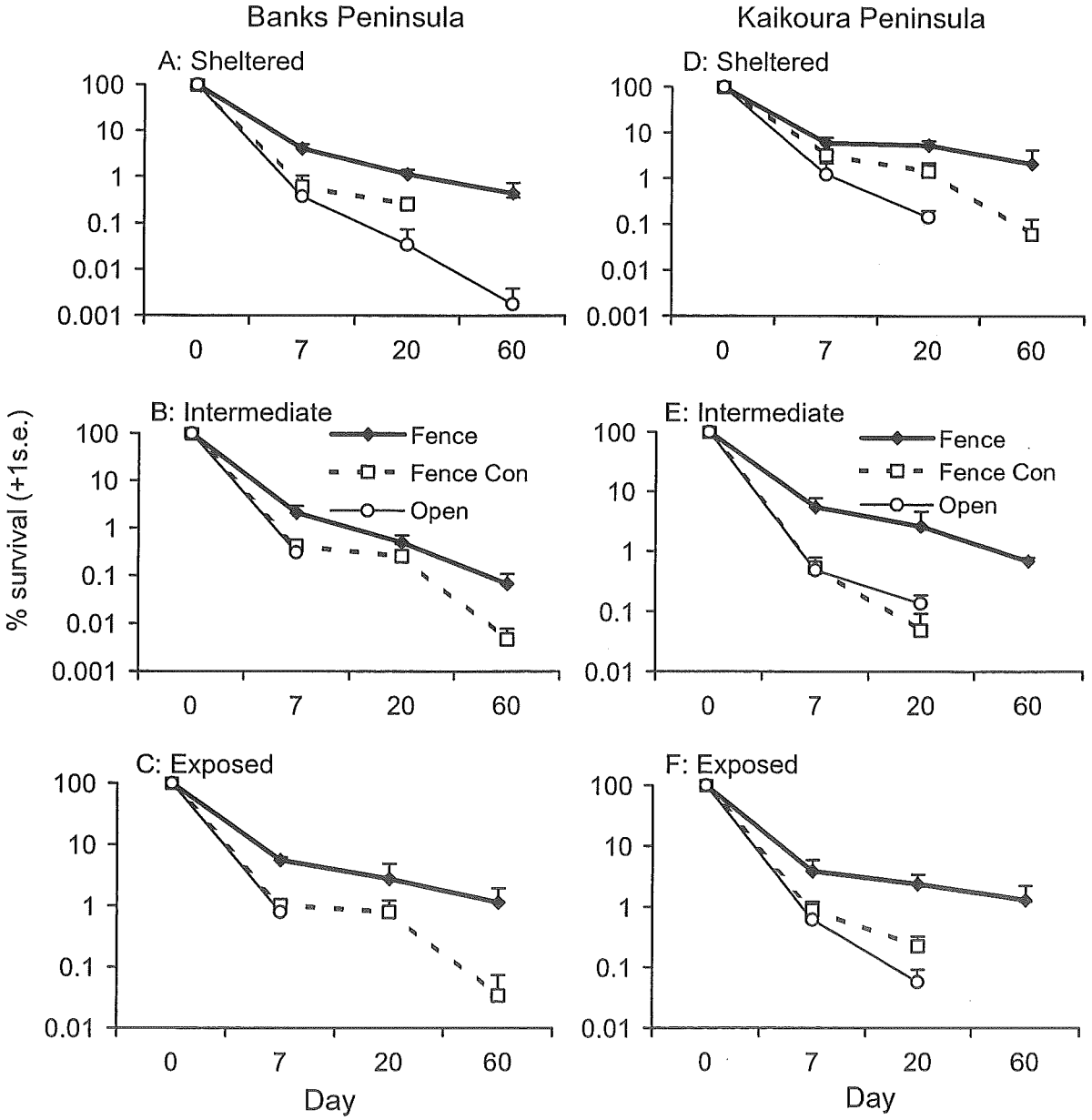

Figure 4.3. Percent survival of *Durvillaea antarctica* germlings over time transplanted across a regional wave exposure gradient from May – July 1999 on Banks Peninsula (A-C) and Kaikoura Peninsula (B-F).

Table 4.3. ANOVA results of survival of *Durvillaea antarctica* germlings transplanted across a regional wave exposure gradient over time. Sites were treated as random. Variances could not be stabilised and results were not considered significant unless $p \leq 0.01$.

	Day 7				*Day 20*		
Factor	df	MS	F-ratio	P	MS	F-ratio	p
Exposure	2	6.503	0.663	0.601	3.897	0.569	0.637
Site	1	10.650	1.628	0.461	9.908	0.893	0.427
Treatment	2	106.436	88.236	**0.011**	38.910	5.589	0.152
Exp x Site	2	9.811	2.192	0.228	6.851	2.526	0.195
Exp x Trt	4	0.845	0.189	0.932	1.451	0.535	0.720
Site x Trt	2	1.206	0.270	0.777	6.961	2.567	0.192
Exp x Site X Trt	4	4.476	1.590	0.190	2.712	1.366	0.258
Error	54	2.816			1.985		

	Day 60			
Factor	df	MS	F-ratio	p
Exposure	2	0.736	1.616	0.382
Site	1	1.378	0.971	0.432
Treatment	2	7.297	5.428	0.156
Exp x Site	2	0.455	1.193	0.392
Exp x Trt	4	0.683	1.789	0.293
Site x Trt	2	1.344	3.524	0.131
Exp x Site X Trt	4	0.382	0.368	0.830
Error	54	1.04		

4.3.1.3 Hormosira regional transplant #2

In the second *Hormosira* RT experiment begun in June 1999, survival of *Hormosira* germlings after 25 days depended on the different magnitudes of treatment effects at exposures and sites (Table 4.4). Fence treatments had consistently greater germling survival than the other treatments. However, at the sheltered Banks Peninsula site and the two exposed sites fence control treatments had greater survival than open plates but overall the two treatments were not significantly different (Tukey HSD, $p > 0.05$). Only the fence treatment at the intermediate Banks Peninsula site had any survival of plants after 25 days (Fig. 4.4B). After 65 days germlings only survived in fences at the sheltered site on Kaikoura Peninsula (Fig.4.4D) and in all treatments at the exposed Banks Peninsula site (Fig. 4.4A-C). After 100 days between 0.05 and 4 percent of *Hormosira*

germlings survived in all treatments at the Exposed Banks Peninsula site (Fig. 4.4C). Only the fence treatment at the sheltered Kaikoura site (Fig.4.4D) and the intermediate Banks Peninsula site (Fig. 4.4B) had germlings after the same period with survival around 3 (1000 plants per plate) and 0.0005 (5 plants per plate) percent respectively.

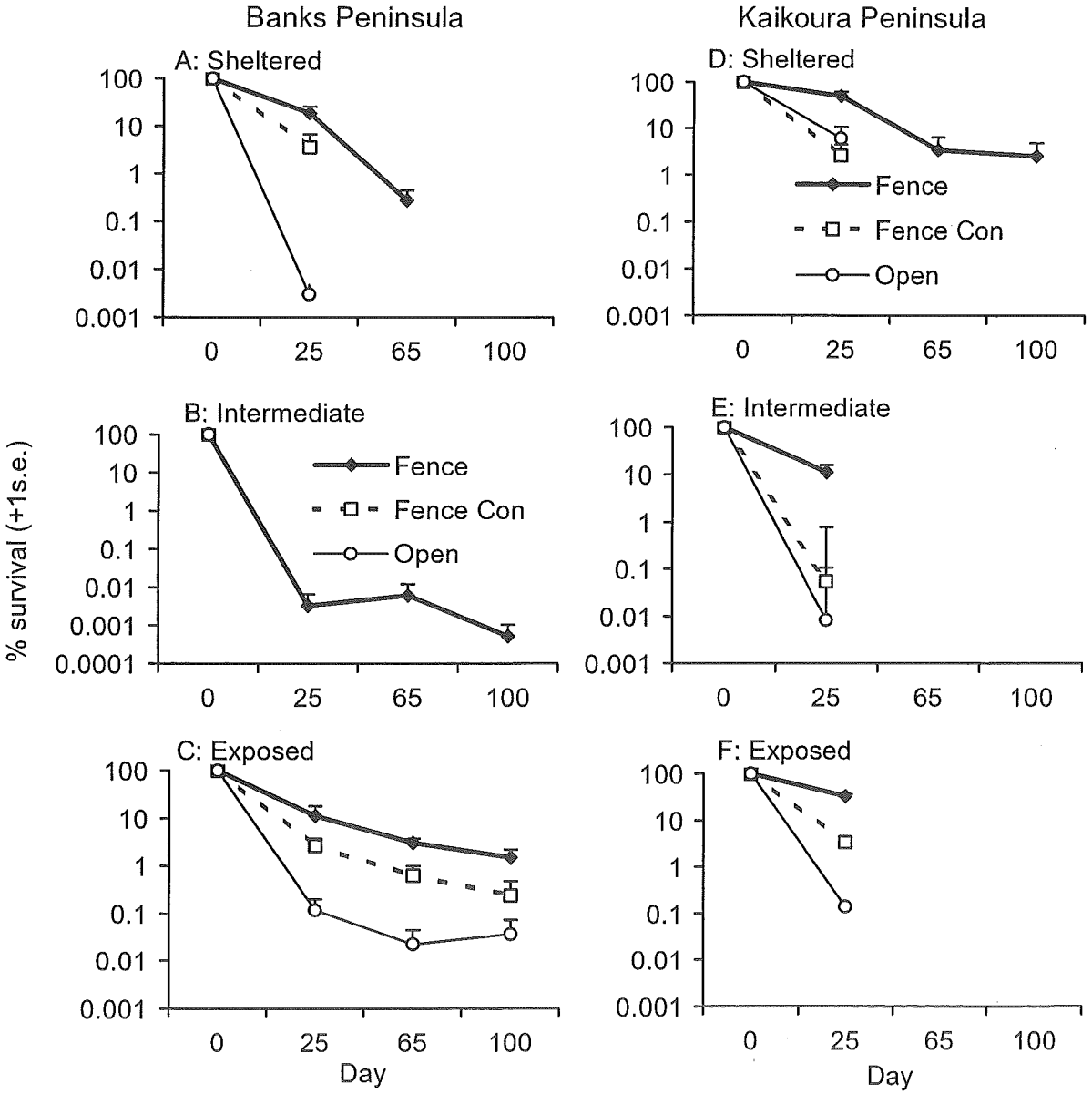

Figure 4.4. Percent survival of *Hormosira banksii* germlings over time transplanted across a regional wave exposure gradient from June - November 1999 on Banks Peninsula (A-C) and Kaikoura Peninsula (B-F).

Table 4.4. ANOVA results of survival of *Hormosira banksii* germlings transplanted across a regional wave exposure gradient in June 1999 over time. Sites were treated as random. Data were square-root arcsine transformed to stabilise variances. All Cochrans tests were not significant.

	Day 25				*Day 65*		
Factor	df	MS	F-ratio	p	MS	F-ratio	p
Exposure	2	0.303	28.691	0.034	0.009	6.153	0.244
Site	1	0.340	1.988	0.289	0.006	0.514	0.660
Treatment	2	0.921	5.523	0.153	0.020	0.533	0.652
Exp x Site	2	0.011	1.643	0.301	0.018	15.703	0.060
Exp x Trt	4	0.087	13.533	0.014	0.005	2.057	0.243
Site x Trt	2	0.167	25.917	0.005	0.001	0.572	0.699
Exp x Site X Trt	4	0.006	0.397	0.810	0.009	0.147	0.867
Error	54	0.016			0.002		

4.3.1.4 Durvillaea regional transplant #2

In the second *Durvillaea* RT experiment begun in July 1999, the survival of *Durvillaea* germlings after 17 days differed significantly across exposures within sites (Table 4.5). Fence treatments had significantly greater germling survival than open plate treatments at Day 17 (Tukey HSD, $p<0.05$). At the intermediate Kaikoura Peninsula site, fence control treatments had greater survival than open plates, indicating a fence effect but overall the two treatments were not significantly different (Tukey HSD, $p>0.05$). After 60 days all fence treatments had *Durvillaea* germlings surviving in them at the Banks Peninsula sites (Fig. 4.5A-C) but at Kaikoura only germlings in the fence treatments at exposed sites survived at Day 60 (Fig. 4.5F). After 60 days at Kaikoura, the open plate treatment at the sheltered site had around 0.1 percent survival (80 plants per plate) and the fence treatment at the exposed site had around 1 percent survival (800 plants per plate) (Fig. 4.5D,F). No *Durvillaea* germlings survived on open plates at Banks Peninsula or in fence control treatments at Kaikoura after 60 days in the field (Fig. 4.5C, E). After 60 days percent survival of *Durvillaea* germlings in fence treatments across exposures at Banks Peninsula ranged from 0.1 percent (80 plants per plate) at the

intermediate site (Fig. 4.5A) to 5 percent (4000 plants per plate) at the exposed site (Fig. 4.5C). One fence treatment plate at the exposed Banks Peninsula site had approximately 0.8 percent survival (c. 50 plants) after 222 days (Fig. 4.5C) that were counted and measured at day 304 and 377. All other treatments had zero percent survival after 222 days.

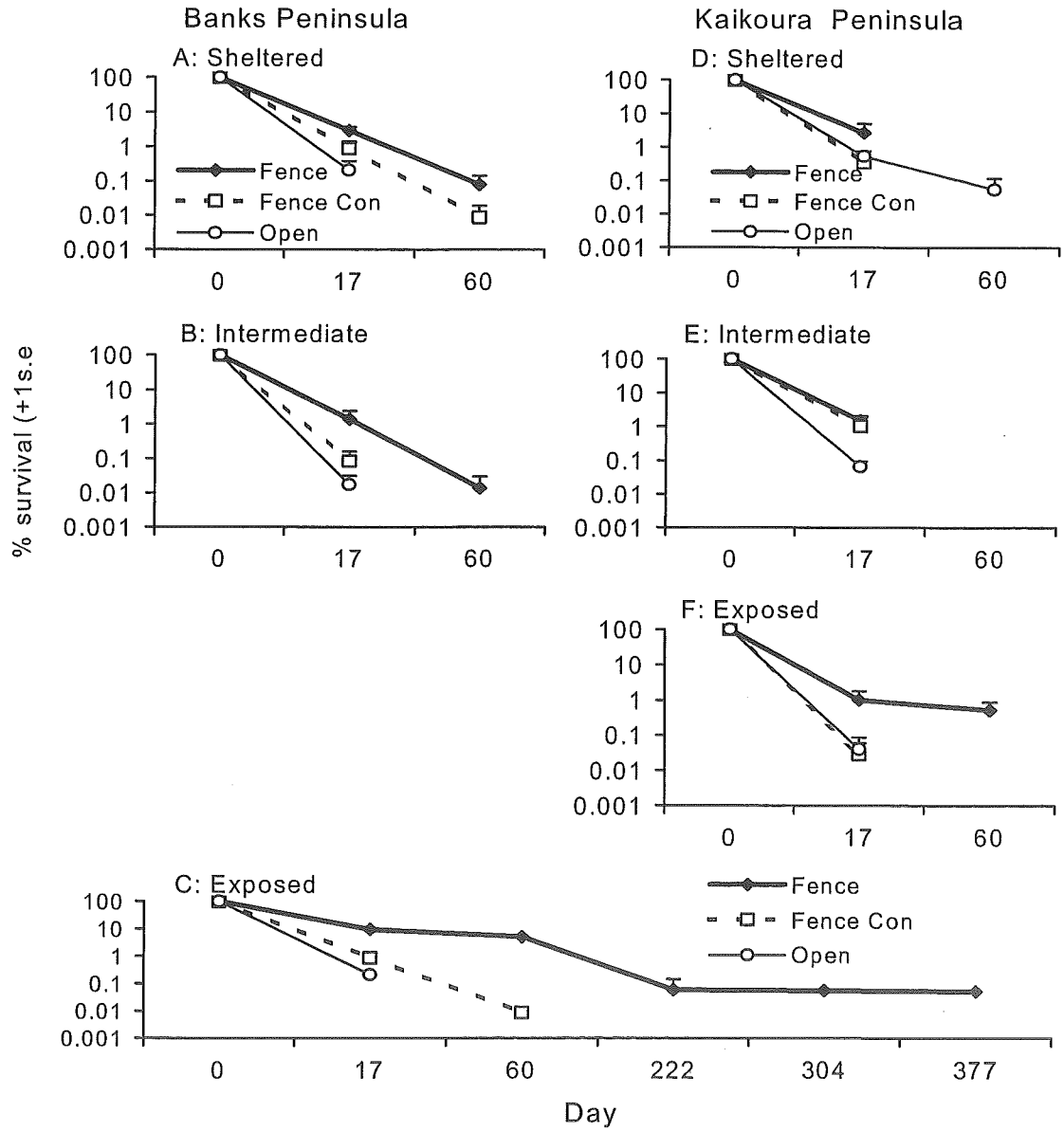

Figure 4.5. Percent survival of *Durvillaea antarctica* germlings over time transplanted across a regional wave exposure gradient from July 1999 - November 2000 on Banks Peninsula (A-C) and Kaikoura Peninsula (B-F). After Day 222 only one fence plate at the exposed BP site had *D. antarctica* germlings surviving.

Table 4.5. ANOVA results of survival of *Durvillaea antarctica* germlings transplanted across a regional wave exposure gradient in July 1999 over time. Sites were treated as random. Day 11 data were square-root arcsine transformed to stabilise variances. Cochrans tests were significant at all other times and results were not considered significant unless $p \leq 0.01$.

	Day 17				*Day 60*		
Factor	df	*MS*	F-ratio	p	MS	F-ratio	p
Exposure	2	95.885	0.707	0.586	6.619	1.485	0.402
Site	1	123.159	0.910	0.441	4.594	0.956	0.522
Treatment	2	30.919	0.431	0.188	6.939	1.469	0.405
Exp x Site	2	135.580	18.124	0.010	4.458	1.019	0.439
Exp x Trt	4	6.563	0.877	0.549	6.718	1.535	0.344
Site x Trt	2	7.177	0.959	0.457	4.724	1.079	0.421
Exp x Site X Trt	4	7.481	0.702	0.594	4.377	26.965	0.000
Error	54	10.652			0.162		

4.3.2 Growth in Regional Transplant experiments

Because experiments using different species were started at different times, caution must be used in comparing growth between species. However, because I repeated experiments at different times using the same species a general comparison of growth of early life stages of *Durvillaea antarctica* and *Hormosira banksii* can be made. Length data from treatments within exposures was pooled because in several cases only 1 replicate from a treatment had germlings surviving on it. ANOVA tests done on lumped data from all RT experiments showed significant differences in lengths between exposures after around 60 days (Table 4.6). In general, *Durvillaea* grew faster than *Hormosira*, particularly at exposed sites, and plants of both species grew slower in experiments started during winter than in experiments started out side winter (Fig. 4.6, 4.7A-F).

Table 4.6. One-way ANOVA tests of mean length of A) *Hormosira* RT 1 day 60, B) *Durvillaea* RT 1 day 60, C) *Hormosira* RT 2 day 65 D) *Durvillaea* RT 2 day 60 germlings across regional wave exposure gradients (site and treatment data were lumped).

Experiment	df	MS	F	p
A) *Hormosira* RT 1				
Exposure	2	0.616	14.63	<0.001
Error	13	0.042		
B) *Durvillaea* RT 1				
Exposure	2	2.270	21.78	<0.001
Error	20	0.104		
C) *Hormosira* RT 2				
Exposure	2	0.130	128.73	<0.001
Error	10	0.001		
D) *Durvillaea* RT 2				
Exposure	2	0.734	6.40	<0.05
Error	9	0.115		

4.3.2.1 Hormosira RT growth

After 56 days *Hormosira* germlings in the RT experiment begun in February 1999 (late summer) were 1.1 mm long at exposed sites, 0.8mm long at sheltered sites and only 0.44mm long at intermediate sites (Fig. 4.6A). Germlings were significantly larger at exposed and sheltered sites than at intermediate sites (Table 4.7A). In contrast, in *Hormosira* RT experiment, begun in June 1999 (winter), germlings were less than half the size of the earlier experiment at 0.5 mm at the sheltered site, 0.36 mm long at the intermediate sites and 0.19 mm at the exposed sites after 65 days (Fig.4.6C). All exposures had significantly different lengths at this time (Table 4.7C). Growth rates (mm/day) were significantly faster in the first *Hormosira* RT experiment than in the second (ANOVA, $F_{1,25} = 26.533$, $p < 0.001$), with plants growing up to three times faster after (Fig.4.6B, D).

Table 4.7. Post-hoc Tukey HSD test results of mean length of A) *Hormosira* RT 1 day 60, B) *Durvillaea* RT 1 day 60, C) *Hormosira* RT 2 day 65 D) *Durvillaea* RT 2 day 60 germlings across regional wave exposure gradients (site and treatment data were lumped).

Exposure	A) *Hormosira* RT 1 (df=13)	B) *Durvillaea* RT 1 (df=20)
SH vs INT	Tukey HSD (**p<0.01**)	Tukey HSD (p>0.05)
SH vs EXP	Tukey HSD (p>0.05)	Tukey HSD (**p<0.001**)
INT vs EXP	Tukey HSD (**p<0.001**)	Tukey HSD (**p<0.001**)
Exposure	C) *Hormosira* RT 2 (df=10)	D) *Durvillaea* RT 2 (df=9)
SH vs INT	Tukey HSD (**p<0.001**)	Tukey HSD (p>0.05)
SH vs EXP	Tukey HSD (**p<0.001**)	Tukey HSD (**p<0.05**)
INT vs EXP	Tukey HSD (**p<0.001**)	Tukey HSD (p>0.05)

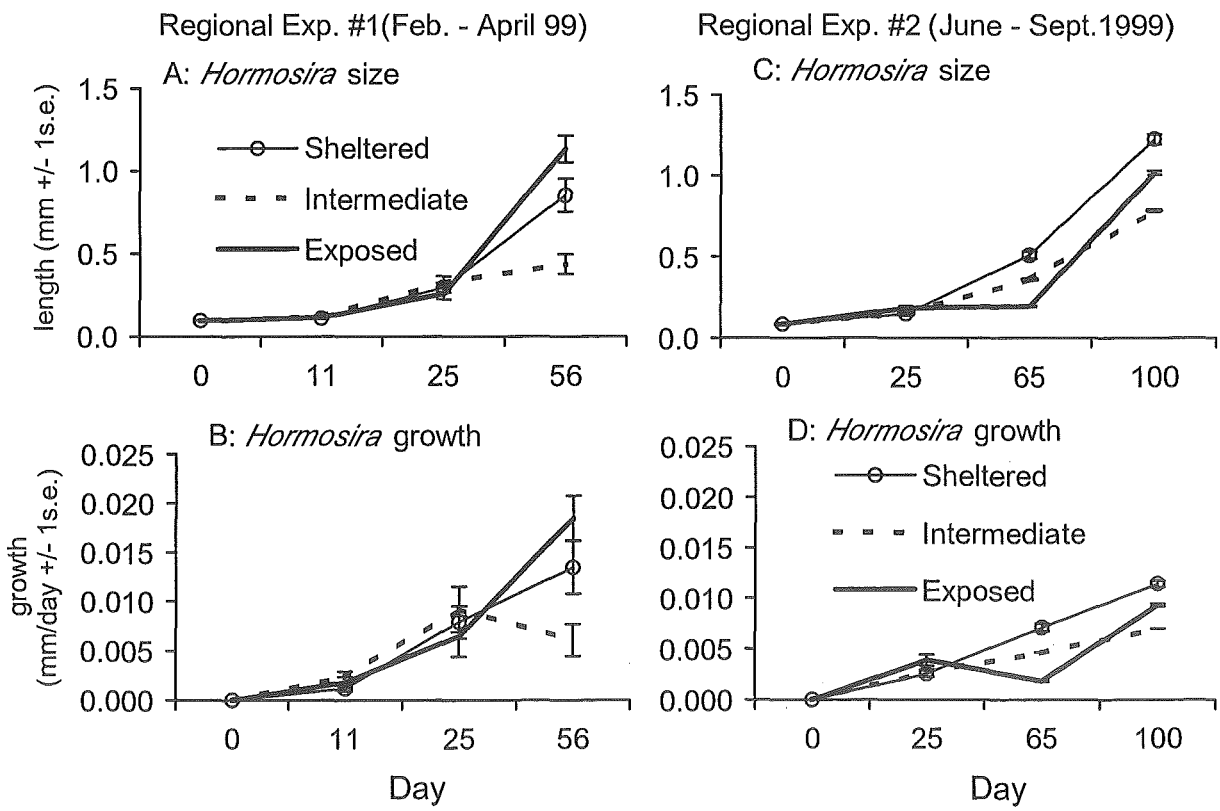

Figure 4.6. Growth and length data from *Hormosira banksii* germlings across exposures in the RT experiments.

4.3.2.2 Durvillaea RT growth

In the first *Durvillaea* RT experiment (May to July 1999), *Durvillaea* germlings grew to 1.8mm at exposed sites and around 0.7mm at intermediate and sheltered sites after 60 days (Fig. 4.7A). Growth rates ranged from 0.01 mm day^{-1} at intermediate sites to 0.25 mm day^{-1} at exposed sites (Fig. 4.7B). Across exposures all lengths were significantly different at Day 60 (Table 4.8B). In contrast, in the second *Durvillaea* RT experiment, (July-September 1999), germlings grew to 2.2 mm at exposed sites, 2 mm at intermediate sites and 1.4 mm at sheltered sites over 60 days. Correspondingly, growth rates for the first 60 days of the second *Durvillaea* RT experiment were higher at the exposed sites at 0.035 mm day^{-1} than at the sheltered and intermediate sites which had growth rates of 0.023 and 0.032 mm day^{-1} respectively (Fig 4.7D). Mean lengths across all exposures were significantly different (Table 4.8D). Overall, lengths were significantly greater in the second *Durvillaea* RT experiment after 60 days than in the first (ANOVA, $F_{1,29} = 24.149$, $p < 0.001$).

Fifty *Durvillaea* recruits survived on one fenced plate at the exposed Banks peninsula site in the second *Durvillaea* RT experiment and their average sizes and growth rates are shown (Fig. 4.7E-F). After 377 day in the field the *Durvillaea* recruits on this plate were c. 200 mm in length. However, all plants were partially grazed by butterfish (*Odax pullus*) at some time in 2000 and remained at around 100mm for several months. Some plants eventually escaped grazing and had grown at rates of almost 0.5 mm day^{-1} by Day 377 (Fig.4.7F).

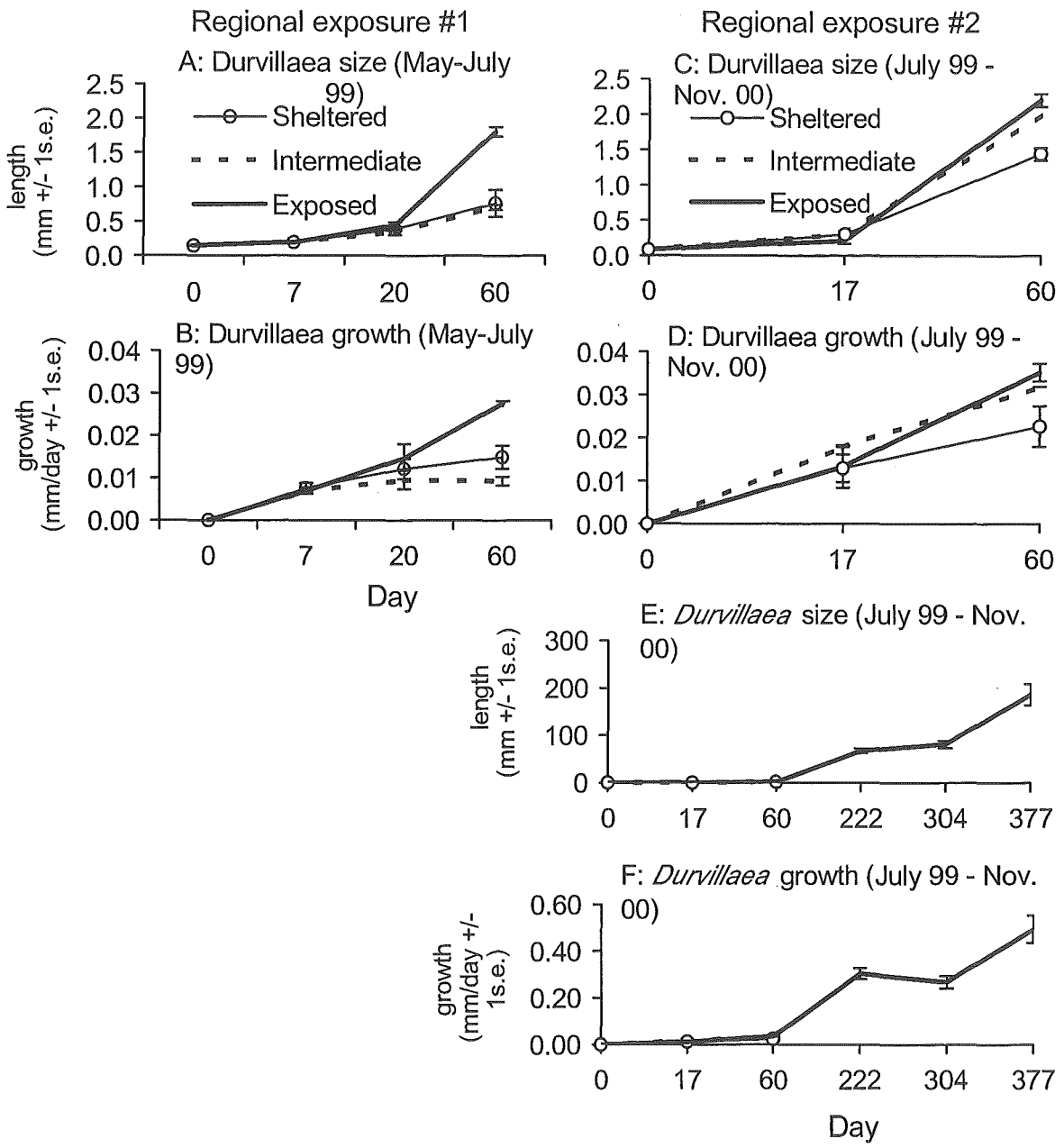

Figure 4.7. Growth and length data from *Durvillaea antarctica* germlings across exposures in the RT experiments. NB: E and D apply to data from plants on one plate at the Banks Peninsula exposed site that survived up to Day 377 in the second *Durvillaea* RT experiment.

4.3.3 Grazing affecting Regional transplant experiments

The invertebrate grazing effect was greatest at the youngest stages of all algal germlings (Fig 4.8A-D). This effect varied considerably between experiments removing less than 1 percent of germlings at the intermediate sites in the second *Durvillaea* RT experiment to 31 percent at the sheltered sites in the second *Hormosira* RT experiment. In all experiments there was clearly a large proportion of mortality due to factors other than grazing. In most fenced treatments, < 1 % of germlings survived after 60 days.

Over the first 11 days of the first *Hormosira* RT experiment the percent of germlings lost to grazing at the sheltered sites was almost double that at the intermediate and exposed sites (Fig. 4.8). Between Day 11 and 25 and 25 and 56 a greater percentage of germlings were lost in the fence treatments than in the fence control treatments. Negative values suggest environmental factors within the fence and fence control treatments were more important during these periods (Fig. 4.8A). The effects of 'within fence' factors increased across exposures between day 11 and day 25 but decreased across exposures between day 25 and 56. This could reflect change in sedimentation and competition from ephemeral algae or changes in environmental variables like desiccation and wave action.

Over the first 7 days of the first *Durvillaea* RT experiment grazing effects increased across exposures ranging from 2 percent at sheltered sites to 3.5 percent at exposed sites (Fig. 4.8B). Between Day 7 and 20 the grazing effect was similar across exposures but was greatest at sheltered sites. Between Day 20 and 60 the effect of grazing was around 1 percent at sheltered and intermediate sites but only 0.35 percent at intermediate sites.

In the second *Hormosira* RT experiment the grazing effect was more than 30 percent at the sheltered sites over the first 25 days (Fig. 4.8C). Less than half that amount was lost to grazing at the exposed sites while only 5 percent was lost to grazing at the intermedaite sites. Between Day 25 - 65 and Day 65-100 high mortality in fence treatments caused grazing effects to decline to 1.5 percent at sheltered sites and less than 1 percent at exposed and intermediate sites.

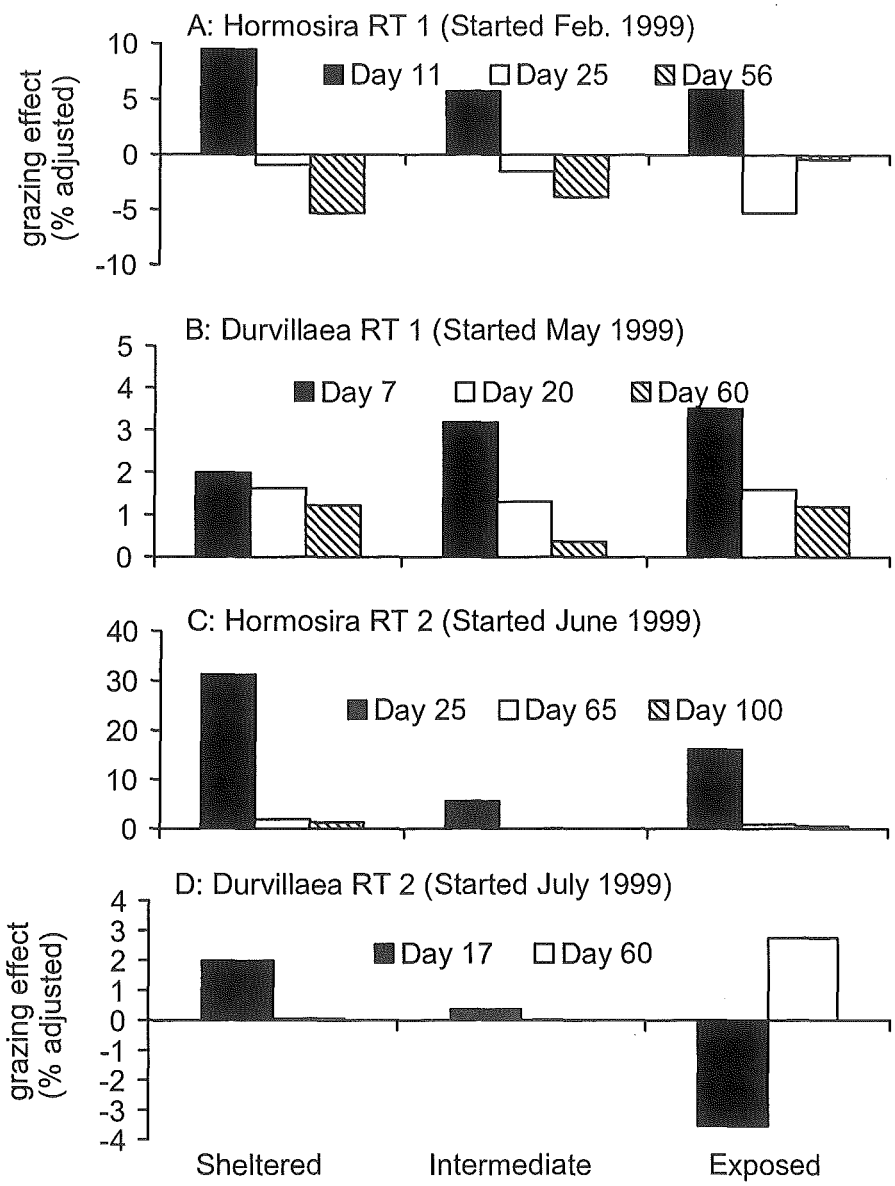

Figure 4.8. Percent of grazing effect (adjusted for fence effect) over all RT experiments. Calculated by subtracting the percent of germlings lost in fenced treatments from the percent lost in fence control treatments then adjusting for the "fence effect' by subtracting the difference between the percent of germlings lost on the fence control and the percent lost on the open plate treatments.

In the second *Durvillaea* RT experiment the effect of grazing was small, ranging from 0.5 percent at the intermediate site to 2 percent at the sheltered site over the first 17 days (Fig. 4.8D). The percent grazed decreased across exposures at this time but increased across exposures after 60 days. The negative value at the exposed sites after 17 days reflects a fence effect (-3.5 percent) caused by higher survival in fence control treatments suggesting factors within fence treatments caused high mortality.

4.3.4 Grazer abundance in RT experiments

Despite the differences in grazing effect across exposure and experiments the total number of grazers did not vary significantly across exposures either on flat rock or in cracks (Table 4.8A,B; Fig. 4.9A,E). However, there was considerable variation between exposures within peninsulas. For example, the sheltered sites at Kaikoura had 24 grazers per $0.25m^2$ while at Banks Peninsula there were only 9 per $0.25m^2$. In cracks grazers were more abundant at the intermediate site on Banks Peninsula which had 16 grazers per 1m of crack while at Kaikoura there were only 5 grazers per 1m length of crack (Fig. 4.9A,E).

The abundance of grazers within morphological groups was tested using a three way ANOVA. Grazer groups, in cracks and on flat rock, were significantly different between peninsulas and exposures, indicated by a significant interaction term (Table 4.9A, B). The differences between sheltered sites was due mostly to the abundance of topshells (Fig. 4.9B), especially *Turbo smaragdus* and *Zeacumentus subcarinatus* at Kaikoura, while limpets (Fig. 4.9C), like *Patelloida corticata* and *Cellana radians*, and chitons (Fig. 4.9D), like *Chiton pelliserpentis* were more abundant on the substratum at Banks Peninsula. At intermediate sites, particularly at the Banks Peninsula site, the most abundant molluscan grazer on the substratum was the topshell *Turbo smaragdus*. The main gastropods at both exposed sites were limpets, particularly *Cellana radians* and several *Patelloida* species and chitons, mainly *Chiton pelliserpentis* and *Onithochiton neglectus* (Fig. 4.9C, D). In 1m long cracks differences between sites within exposures were mainly due to the abundance of topshells (Fig, 4.9E), particularly *Turbo smaragdus*

at the intermediate site on Banks Peninsula. Limpets, mainly *Cellana radians* were also most abundant at the Banks peninsula sites where there were always 1 -2 per 1m of crack. Chitons, mainly *Chiton pelliserpentis* were most abundant at the intermediate site at Banks Peninsula at 3 per 1m of crack, but none were found at the intermediate site in Kaikoura.

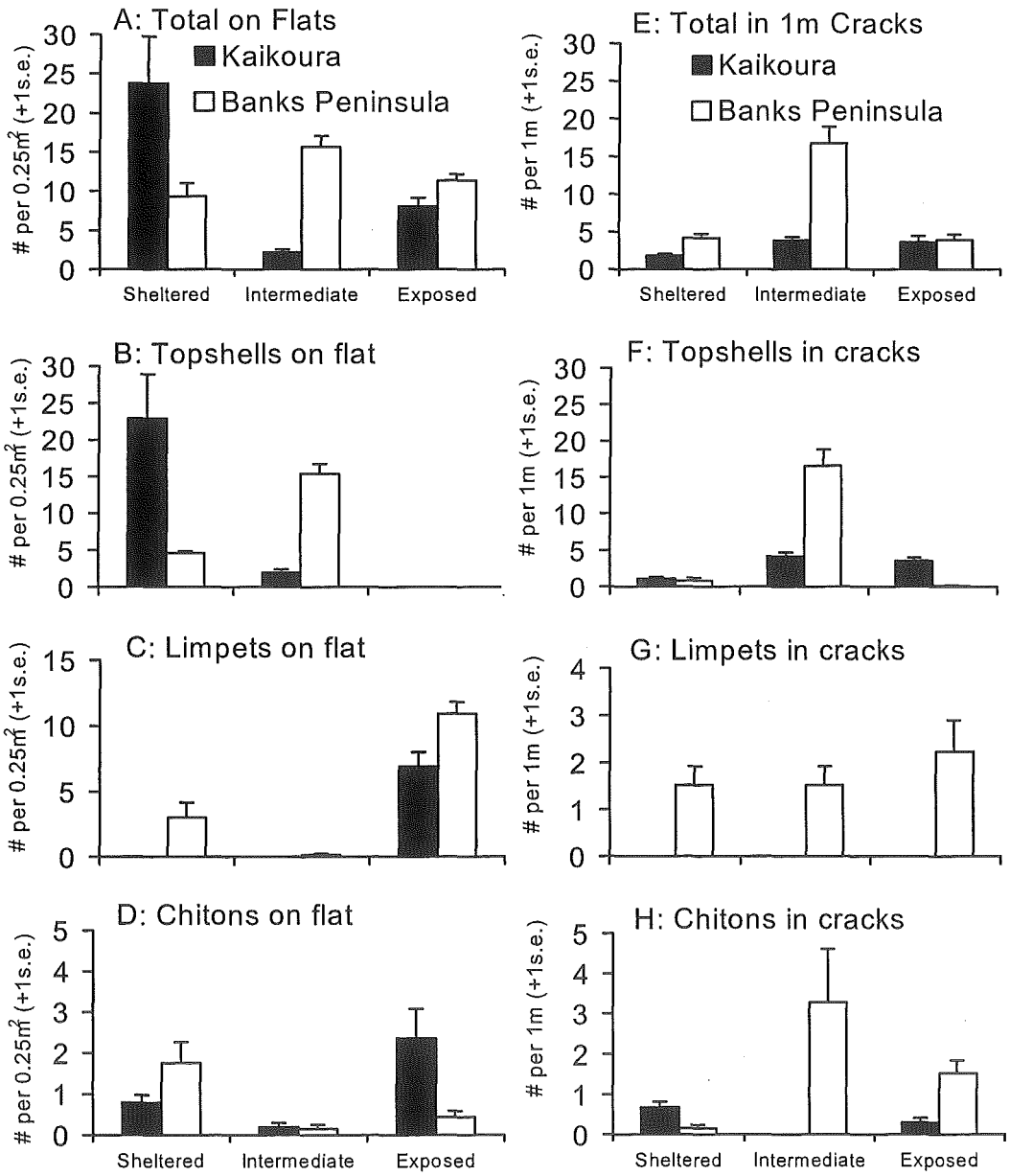

Figure 4.9. Total abundance of invertebrate grazers in 1m long cracks and 0.25m^2 quadrats on flat rock (A, E) and the abundance of Topshells (B,F), Limpets(C,G) and Chitons (D,H) across exposures in RT experiments.

Table 4.8. ANOVA of the effect of wave exposure and peninsula (random) on the abundance of invertebrate molluscan grazers A) per 0.25m^2 on the flat substratum and B) in 1 m long cracks in the low tidal-zone across a regional-scale wave exposure gradient. NB: A) Cochrans C test was significant. B) Data were log transformed to stabilise variances and Cochran C test not significant.

Factor	df	MS	F-ratio	p	MS	F-ratio	p
A) Flat Rock					*B) Cracks*		
Exposure	2	909.53	0.353	0.739	815.360	1.452	0.408
Peninsula	1	35.53	0.014	0.917	993.307	1.769	0.315
Exp x Peninsula	2	2577.49	12.957	0.000	561.627	16.616	0.000
Residual	144	198.93			33.801		

Table 4.9. ANOVA results of invertebrate grazer numbers A) in 1m long cracks and B) per 0.25 m^2 of flat rock testing the effects of Exposure, Peninsulas and Grazer groups (Topshells, Limpets and Chitons) across a regional wave exposure gradient. Peninsulas were treated as fixed. Variances could not be stabilised and Cochrans tests were significant.

Factor	df	MS	F-ratio	P	MS	F-ratio	P
A) 1m Cracks					B) Flat		
Exposure	2	244.927	18.1736	0.000	4.706	10.545	0.0000
Peninsula	1	249.389	18.505	0.000	13.073	29.295	0.0000
Grazer group	2	659.727	48.952	0.000	22.519	50.463	0.0000
Exp x Pen	2	234.016	17.364	0.000	3.642	8.162	0.0003
Exp x Grz	4	586.873	43.546	0.000	52.854	118.443	0.0000
Pen x Grz	2	368.002	27.306	0.000	5.187	11.624	0.0000
Exp x Pen x Grz	4	194.169	14.407	0.000	9.764	21.880	0.0000
Residual	432	13.477			0.446		

4.3.5 RT Thermistor data

Thermistor data taken during the second *Hormosira* and the second *Durvillaea* regional exposure experiments show that temperature ranges were similar across exposures (Fig. 4.10A-E). The exception was the exposed Raramai site where greater wave action and shading from surrounding hills reduced temperature extremes (Fig 4.10B). Peaks in temperature close to times when experiments were started relate to low tide series and are the probable cause of high mortality within the first few weeks of these experiments. During the second *Hormosira* RT experiment, temperatures at the sheltered Devauchelles site ranged between 4°C and 18°C in the first 25 days and between 0°C on 11/7/99 to 30°C 1/9/99 up to day 65 (Fig. 4.10A). Similar ranges in temperatures were recorded at the same times at the sheltered Mudstone Bay site, although temperatures did not drop to 0°C (Fig. 4.10B). During the first 25 days of the second *Hormosira* RT experiment temperatures ranged from 2 °C to 16°C at the intermediate Carpark site and between 2 °C and 21°C for the first 17 days of the second *Durvillaea* RT experiment (Fig. 4.10C). The exposed Boulder Bay site had greater range of temperatures, between 4°C and 21°C, during the first 25 days of the *Hormosira* experiment and ranged between 5°C and 22°C for the first 17 days of the *Durvillaea* experiment (Fig. 4.10A). At the exposed Raramai site temperatures ranged between 8 and 12°C for the first 25 days of the second *Hormosira* RT experiment but were more variable during the first 17 days of the second *Durvillaea* RT experiment when they ranged between 6°C to 24°C (Fig.4.10B).

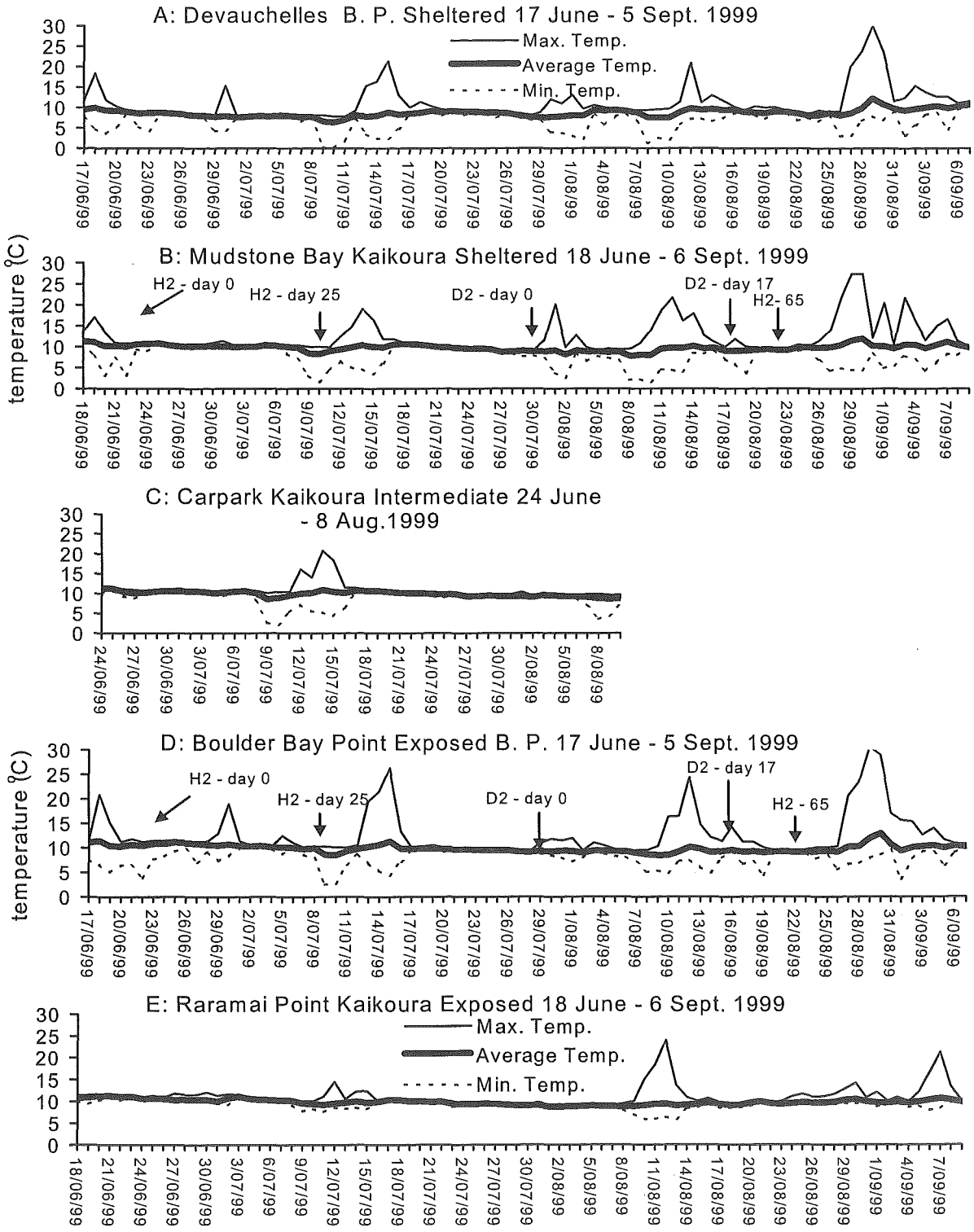

Figure 4.10. Average, maximum and minimum temperature data in (°C) from thermistors at sites across the RT wave exposure gradient exposure gradient from 17 June 1999 – 17 September 1999. Labels (H2, D2) relate to the second *Hormosira* and *Durvillaea* RT experiments and the days at which they were monitored. Thermistors and plates were exposed during some low tides.

4.3.6. Hemispheric comparisons: Local-scale transplant experiments

4.3.6.1 Durvillaea antarctica local-scale transplant

In the *Durvillaea antarctica* LT experiment begun in August 2001, survival was not affected by caging treatments after 24 hours but exposures had different magnitudes of effects at each site (Table 4.10). This interaction effect resulted from the intermediate site at First Bay having significantly greater survival than the sheltered site (Fishers LSD, $p=0.014$). A large storm event on Day 7 prevented sampling and destroyed plates and treatments from the Seal Reef exposed site. Consequently, only First Bay data were analyzed from Day 7 onwards. After 7 days there was a significant difference in survival of *Durvillaea antarctica* germlings across exposures (Table 4.10). Survival was greater at the sheltered site with around 45 percent of germlings surviving while at the intermediate site less than 35 percent of germling survived in fences (Fig. 4.11A-F). At the exposed site after 14 days less than 5 percent of *Durvillaea* germlings survived in fence treatments relating to c.100 per plate.

Table 4.10. ANOVA results of survival of *Durvillaea antarctica* germlings transplanted across a local-scale wave exposure gradient over time. Sites were treated as random (A). Day 7 (B) and 14 (C) data are First Bay only. A treatment average was substituted for a lost fence control replicate and the degrees of freedom adjusted accordingly. All Cochran's tests not significant.

A) *Day 1*	*First Bay and Seal Reef*			
Factor	df	MS	F-ratio	p
Exposure	2	1700.0.95	0.890	0.529
Site	1	1020.930	0.553	0.541
Caging Treatment	2	1203.732	6.060	0.142
Exp x Site	2	1909.833	7.273	0.047
Exp x Treat	4	612.282	2.332	0.216
Site x Treat	2	198.641	0.756	0.526
Exp x Site x Treat	4	262.603	0.242	0.913
Error	36	1086.103		
B) *Day 7*	*First Bay only*			
Factor	df	MS	F-ratio	p
Exposure	2	1211.685	4.103	0.034
Caging Treatment	2	1052.373	3.564	0.050
Exp x Treat	4	74.162	0.251	0.905
Error	17	295.314		
C) *Day 14*	*First bay only*			
Factor	df	MS	F-ratio	p
Exposure	2	928.048	3.799	0.042
Caging Treatment	2	1428.860	5.849	0.011
Exp x Treat	4	638.067	2.612	0.070
Error	17	244.278		

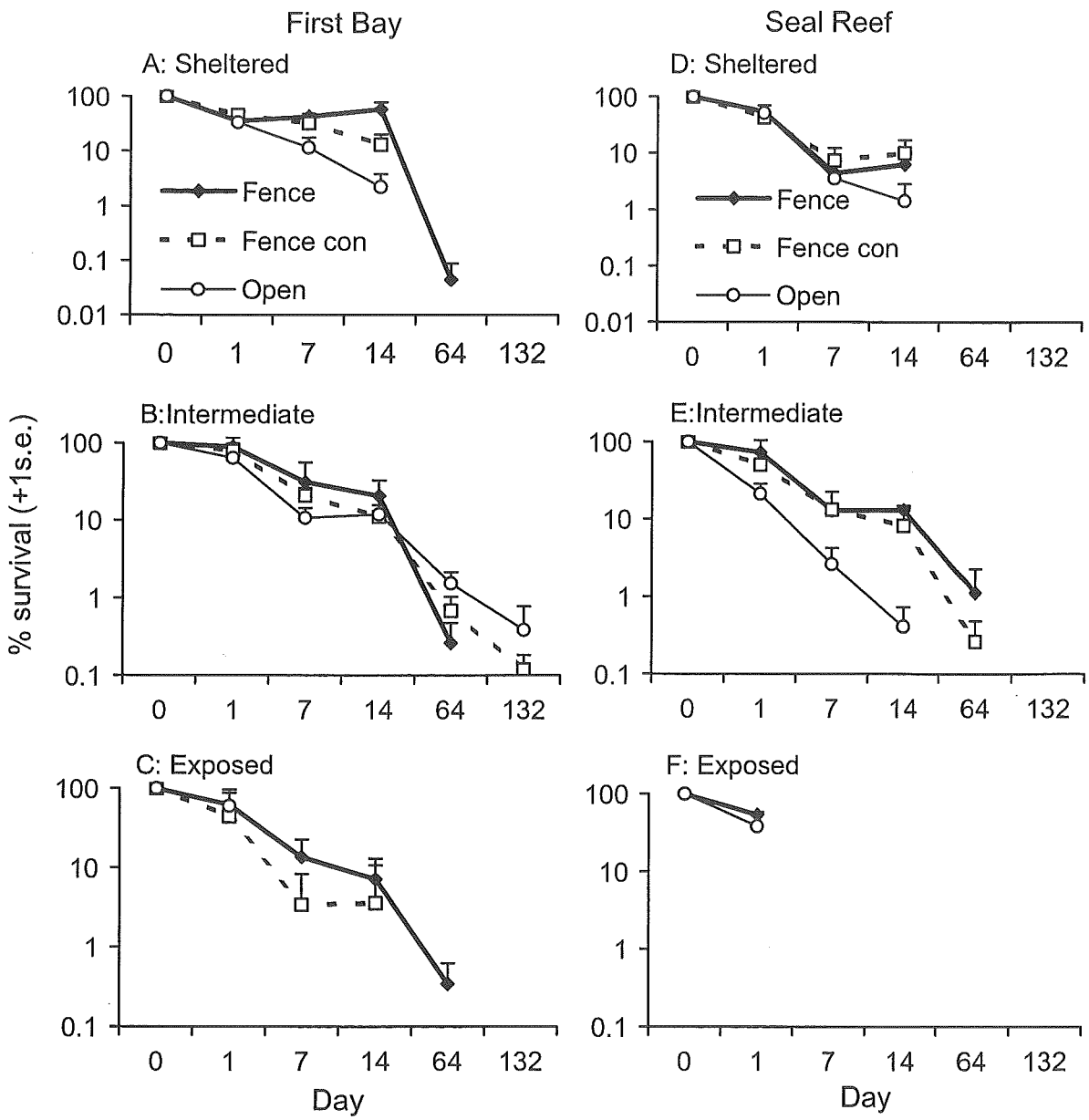

Figure 4.11. Percent survival of *Durvillaea antarctica* germlings over time transplanted across a local-scale wave exposure gradient from August - December 2001 at First Bay (A-C) and Seal Reef (D-F) on Kaikoura peninsula. Plates and caging treatments at the exposed Seal Reef site were destroyed or could not be sampled after Day 7.

4.3.6.2 Hormosira local-scale transplant

In the *Hormosira banksii* LT experiment begun in January 2002 after 2 days in the field, survival of germlings depended on exposure but exposure had different magnitudes of effect between sites (Table 4.11). This effect was due to significant differences in the survival of germlings on plates at the sheltered and intermediate sites. At First Bay plates at the sheltered site had c. 52 percent survival while at Seal Reef the sheltered site had c.75 percent survival. At the intermediate sites those in First Bay had greater survival (c.81 percent) compared to Seal Reef (64 percent). After 9 days, there was a significant difference between the effects of treatments. For example, fence and fence control treatments had around 40 percent survival at the intermediate First Bay site but only 12 percent at Seal Reef. In general, grazer exclusion plates had greatest survival over the first 20 days (Fig. 4.12A-F) but sites continued to have different magnitudes of treatment effects (Table 4.11). For example, survival within fence control treatments at the intermediate First Bay sites was around 35 percent but was 5 percent at Seal Reef. At the end of the experiment there were no significant treatment, site or exposure effects on the survival of *Hormosira* germlings (Table 4.11). However, the fence and fence control treatments at the intermediate First Bay site had around 5 percent survival, which related to around 500 plants per plate.

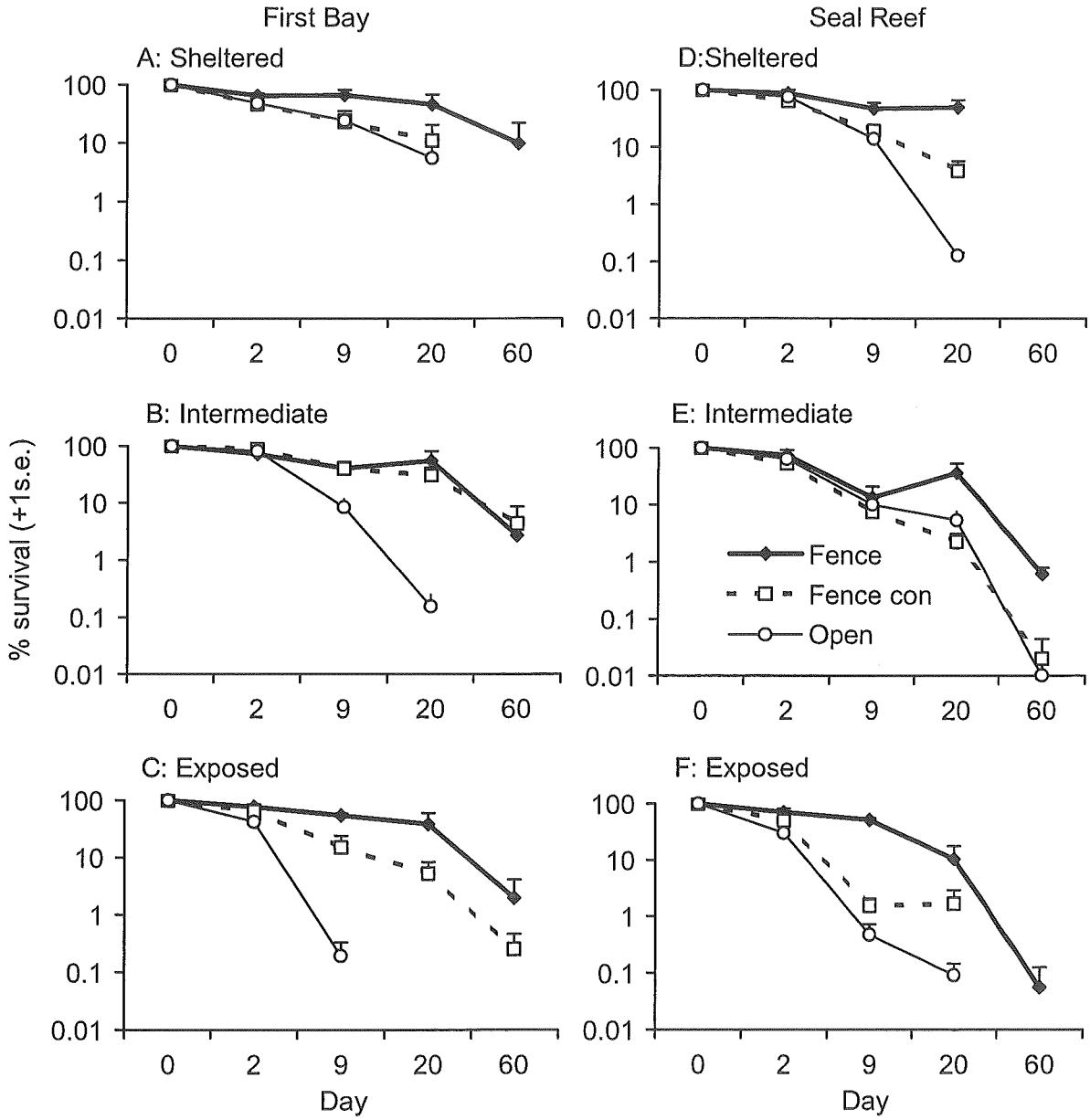

Figure 4.12. Percent survival of *Hormosira banksii* germlings over time transplanted across a local-scale wave exposure gradient from January - March 2002 at First Bay (A-C) and Seal Reef (D-F) on Kaikoura peninsula.

Table 4.11. ANOVA results of survival of *Hormosira banksii* germlings transplanted across a local-scale wave exposure gradient over time. Sites were treated as random and nested in Exposures. Day 9 data were square-root transformed and Day 20 and 60 data were arcsin transformed. Cochran's tests were not significant. A treatment average was substituted for a lost fence replicate at day 60.

	Day 2				*Day 9*		
Factor	df	MS	F-ratio	p	MS	F-ratio	p
Exposure	2	0.418	0.612	0.622	18.061	6.942	0.126
Site	1	0.084	0.110	0.765	21.220	5.735	0.245
Caging Treatment	2	0.544	5.166	0.162	75.373	19.086	0.050
Exp x Site	2	0.689	12.246	0.020	2.602	0.913	0.472
Exp x Treat	4	0.240	4.261	0.095	12.127	4.254	0.095
Site x Treat	2	0.106	1.872	0.267	3.949	1.385	0.349
Exp x Site x Treat	4	0.563	0.464	0.762	2.851	2.301	0.077
Error	36	0.121			1.239		
	Day 20				*Day 60*		
Factor	df	MS	F-ratio	p	MS	F-ratio	p
Exposure	2	0.099	4.593	0.179	0.001	1.027	0.493
Site	1	0.142	5.278	0.365	0.006	3.490	0.402
Caging Treatment	2	0.869	23.562	0.041	0.003	1.123	0.452
Exp x Site	2	0.022	0.683	0.556	0.001	0.463	0.659
Exp x Treat	4	0.035	1.117	0.459	0.002	0.864	0.555
Site x Treat	2	0.037	1.169	0.398	0.003	1.534	0.320
Exp x Site x Treat	4	0.032	0.790	0.540	0.002	0.865	0.494
Error	36	0.040			0.002		

4.3.6.3 Fucus gardneri LT experiment

Fucus gardneri germlings transplanted across exposures in June 2001 did not have different survival rates after 24 hours in the field (Table 4.12). However, at Day 1 there were significant caging treatment effects on germling survival. For example, open plates had lower survival than fence and fence control treatments at both sites. At Day 4, exposures had different magnitudes of effects at each site. This effect was due to the significantly lower survival of germlings at the sheltered Fogarty Creek site, where plates were found covered with sand (Tukey HSD, $P<0.05$). Caging treatments also had different magnitudes of effect at each site at Day 4. For example, the open plate

treatments at the exposed sites at Depoe Bay had less than 5 percent of germlings survived after 4 days but at Fogarty creek 55 percent survived. After 14 days, neither exposure, site or treatment had any effect on germling survival (Fig. 4.13D-F).

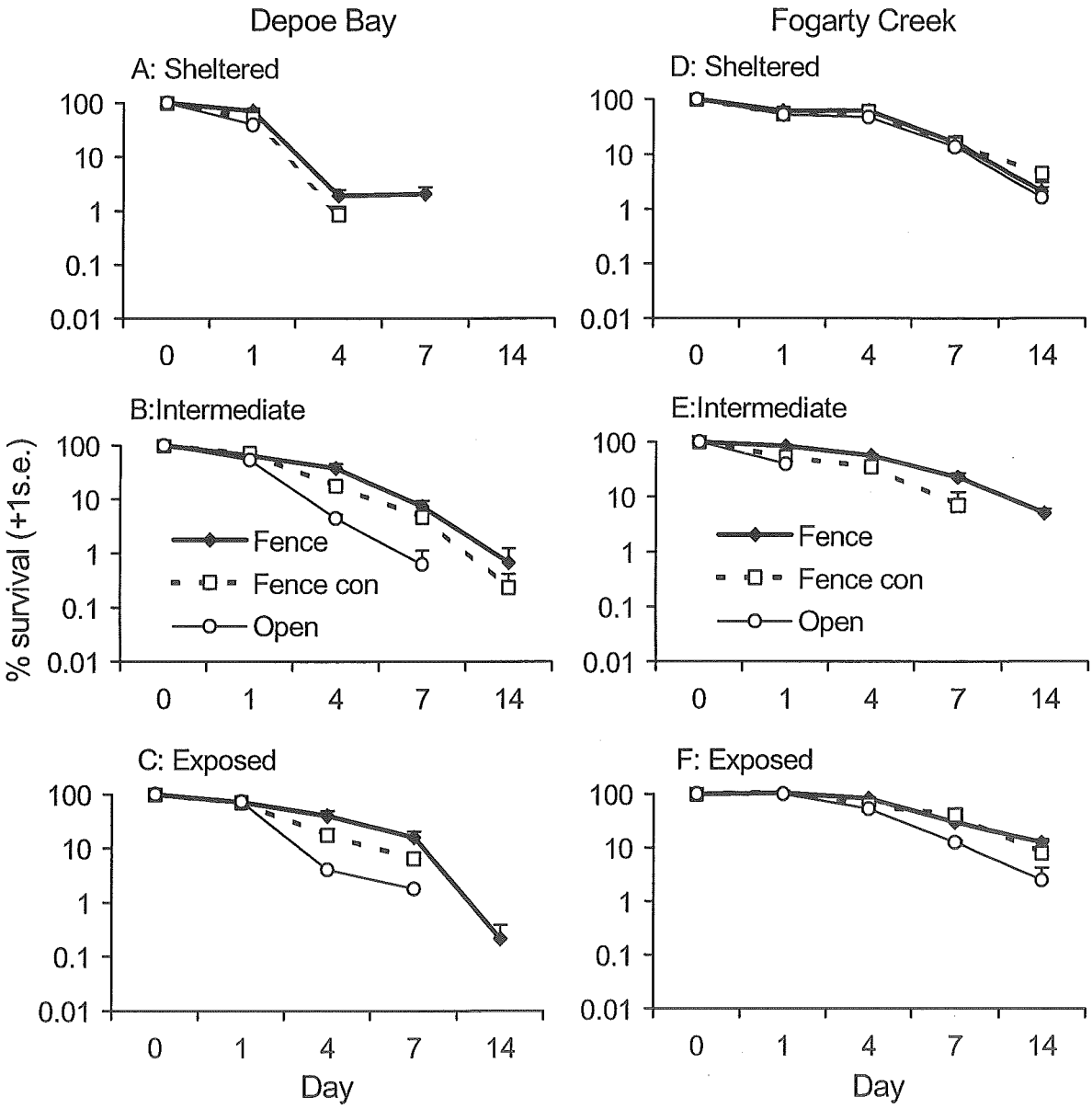

Figure 4.13. Percent survival of *Fucus gardneri* germlings over time transplanted across a local-scale wave exposure gradient from June – August 2001 at Depoe Bay (A-C) and Fogarty Creek (D-F).

Table 4.12. ANOVA results of survival of *Fucus gardneri* germlings transplanted across a local-scale wave exposure gradient over time. Sites were treated as random. Day 4, 7, 14 data were $\log_{(n+1)}$ transformed to stabilize variances. All Cochran's tests not significant.

		Day 1			*Day 4*		
Factor	df	MS	F-ratio	p	MS	F-ratio	p
Exposure	2	1.037	9.213	0.098	7.148	1.028	0.493
Site	1	0.450	7.107	0.357	56.988	5.577	0.085
Caging Treatment	2	0.248	55.069	**0.018**	4.994	2.760	0.266
Exp x Site	2	0.113	2.095	0.239	6.953	70.928	**0.001**
Exp x Treat	4	0.085	1.577	0.335	0.192	1.955	0.266
Site x Treat	2	0.005	0.084	0.921	1.810	18.459	**0.010**
Exp x Site x Treat	4	0.054	1.522	0.217	0.098	0.624	0.649
Error	36	0.04			0.157		
		Day 7			*Day 14*		
Factor	df	MS	F-ratio	p	MS	F-ratio	p
Exposure	2	3.338	3.241	0.236	0.323	0.501	0.666
Site	1	51.380	52.593	**0.030**	16.046	10.835	0.074
Caging Treatment	2	7.523	32.966	**0.029**	2.23	1.789	0.359
Exp x Site	2	1.030	3.662	0.125	0.645	1.568	0.314
Exp x Treat	4	0.724	2.574	0.191	0.673	1.635	0.323
Site x Treat	2	0.228	0.811	0.506	1.247	3.033	0.158
Exp x Site x Treat	4	0.281	0.267	0.899	0.411	0.827	0.517
Error	36	1.055			0.497		

4.3.6.4 Pelvetiopsis LT experiment

After 24 hours in the field *Pelvetiopsis* germlings transplanted across a local-scale exposure gradient in June 2001 (Boreal Spring-Summer) had significantly different survival rates across exposures (Table 4.13). For example, there was lower survival at both sheltered sites where fenced treatments had around 55 percent survival (Fig. 4.14A,D). A large influx of sand was observed at the sheltered Fogarty Creek site during this time. In contrast, there was 80 percent survival at both exposed sites (Fig. 4.14C, F) and between 80 and 100 percent survival at the two intermediate sites (Fig. 4.14B, E). However, the effect of exposure had different magnitudes of effect for each caging treatment and at each site (Table 4.13). These significant interactions resulted from lower survival in open plate treatments at both sheltered sites and greater survival at the intermediate and exposed Fogarty Creek sites than at their respective Depoe bay sites (Fig 4.14E,F & B,C). Caging treatments also had different a magnitude of effect at each site. This was largely due to significantly lower survival of fence control treatments at Depoe Bay (Fig 4.14A, B, C). After 4 days, exposure had different magnitudes of effects at the two sites (Table 4.13). Greater survival of germlings at the intermediate site at Fogarty creek was largely responsible for this interaction effect. Caging treatments continued to have different magnitudes of effects at each site after 4 days (Table 4.13). Overall, lower survival of germlings in cage treatments at Fogarty Creek was responsible for this effect. At Day 8 exposure again had different magnitudes of effects at each site. The source of this interaction effect was the similar survival of germlings at all exposures at Depoe Bay and significantly different survival between exposures at Fogarty Creek, where survival was greater at the intermediate sites than the exposed and sheltered sites. After 14 days survival between exposures remained different at each site. For example, sand scour appeared to remove all plants at the sheltered Fogarty Creek site but around 5 percent of plants remained on all treatments at the sheltered Depoe Bay site (Table 4.13). Furthermore, at the exposed site around 10 percent of plants survived on Fence and

Fence control treatments at the Fogarty Creek exposed site but less than 1 percent survived on the same treatments at Depoe Bay (Fig. 4.14C,F).

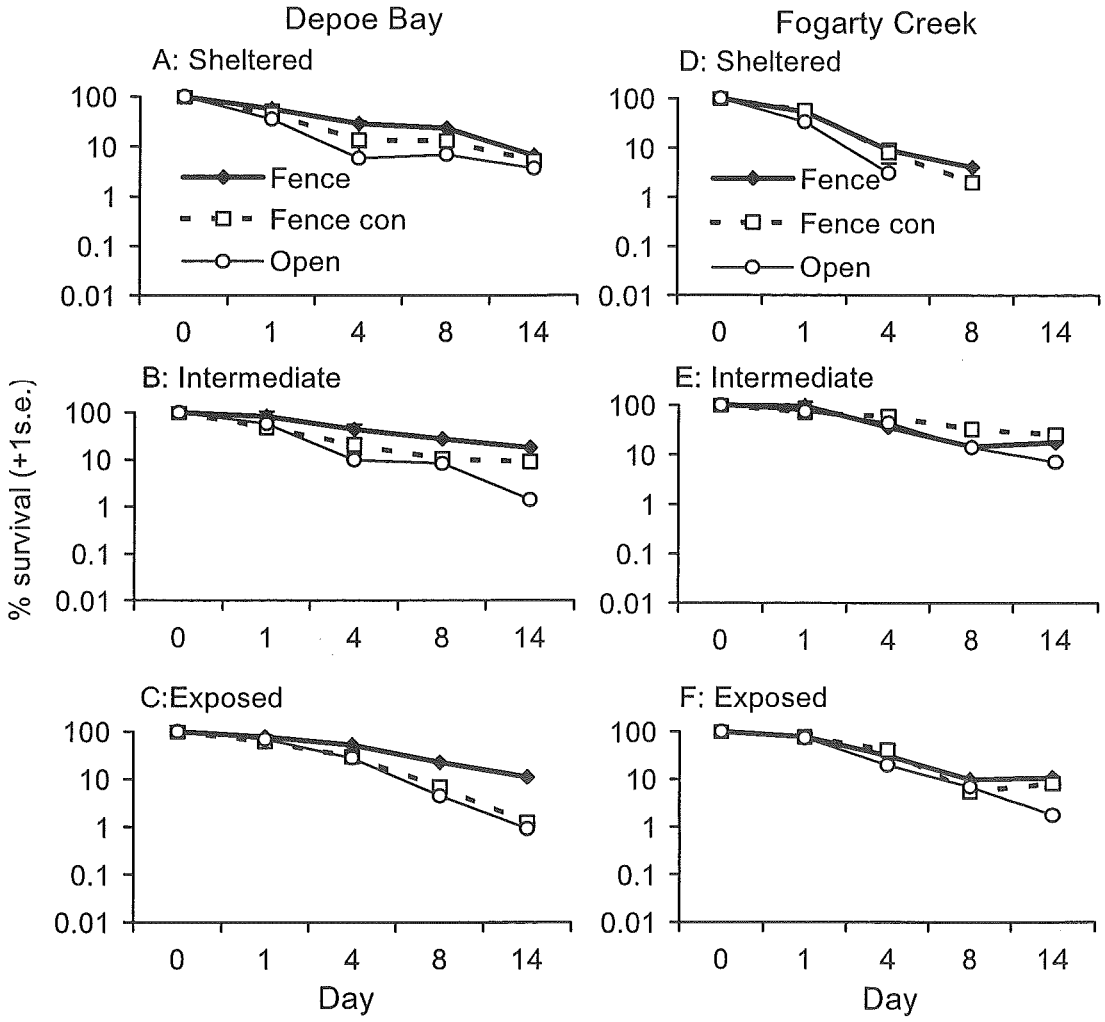

Figure 4.14. Percent survival of *Pelvetiopsis limitata* germlings over time transplanted across a local-scale wave exposure gradient from May 2002 at Depoe Bay (A-C) and Fogarty Creek (D-F) on the Oregon Coast.

Table 4.13. ANOVA results of survival of *Pelvetiopsis limitata* early post-settlement stages transplanted across a local-scale wave exposure gradient over time. Sites were treated as random. Day 1, 4,8 and 14 data were square-root transformed. All Cochrans tests were non-significant.

		Day 1			*Day 4*		
Factor	df	MS	F-ratio	p	MS	F-ratio	p
Exposure	2	19.912	25.409	0.038	46.478	3.367	0.229
Site	1	3.111	1.297	0.333	0.005	0.000	0.989
Treatment	2	5.718	3.321	0.231	14.696	1.197	0.455
Exp x Site	2	0.784	7.355	0.046	13.804	8.430	0.037
Exp x Treat	4	1.511	14.182	0.012	0.649	0.396	0.804
Site x Treat	2	1.722	16.62	0.012	12.273	7.495	0.044
Exp x Site x Treat	4	0.107	0.072	0.990	1.637	0.939	0.452
Error	36	1.482			1.743		
		Day 8			*Day 14*		
Factor	df	MS	F-ratio	p	MS	F-ratio	p
Exposure	2	14.938	1.148	0.466	21.757	1.835	0.353
Site	1	14.574	0.798	0.434	0.296	0.021	0.895
Treatment	2	12.645	1.974	0.336	13.466	4.832	0.171
Exp x Site	2	13.010	11.256	0.023	11.857	16.908	0.011
Exp x Treat	4	16.292	1.410	0.374	3.880	5.533	0.063
Site x Treat	2	6.406	5.542	0.070	2.787	3.974	0.112
Exp x Site x Treat	4	1.156	0.919	0.463	0.701	0.661	0.623
Error	36	1.258					

4.3.7 Growth in local-scale transplant experiments

Durvillaea antarctica LT

At 14 days there was no difference in the length of *Durvillaea antarctica* plants across wave exposures (Table 4.14A). However, plant lengths were significantly different across different exposures after 64 days (Table 4.14E; Fig 4.15A). Plants were significantly longer at exposed sites (Tukey HSD: Exposed vs. Sheltered, $p<0.05$; Exposed vs. Intermediate, $p<0.05$), but there was no difference in lengths between intermediate and sheltered sites (Tukey HSD, $p>0.05$). At Day 64 plants had grown at around 0.07 mm day^{-1} (Fig. 4.15B). After 132 days *Durvillaea* germlings at the exposed sites were almost

double the size of those at the intermediate sites and plants had grown at almost 0.3 mm day^{-1} (Fig 4.15C).

Hormosira banksii LT

The lengths of *Hormosira banksii* germlings were not significantly different across exposures after 20 days (Table 4.14B). Lengths were highly variable across exposures but there were no significant differences among exposures after 64 days (Table 4.14F). Germlings reached approximately 1mm in length after 60 days (Fig. 4.15E), growing at only c. 0.013 mm day^{-1} (Fig.4.15F).

Fucus gardneri LT

The lengths of *Fucus* germlings transplanted across wave exposures were significantly different across exposures after 14 days (Fig. 4.16A; Table 4.14C). Plants were significantly longer at exposed sites than at sheltered and intermediate sites (Tukey HSD: Exposed vs. Intermediate, $p<0.001$; Exposed vs. Sheltered, $p<0.05$). There was no difference in lengths of plants at the sheltered and intermediate sites at this time (Tukey HSD:, Sheltered vs. Intermediate $p>0.05$). Correspondingly, growth over the first 14 days was greatest at exposed sites at c.0.01 mm day^{-1} (Fig. 4.16B). Between Day 14 and Day 82 a large storm removed all plates from the exposed sites. However, at the intermediate sites plants had grown at 0.07 mm day^{-1} while plants at the sheltered site had grown at less than 0.02mm day^{-1} (Fig. 4.16D). These growth rates related to germlings of up to 5mm in length at intermediate sites and only 1mm at sheltered sites.

Pelvetiopsis limitata LT

Germlings of *Pelvetiopsis limitata* grew to significantly different lengths across exposures after 14 days (Table 4.14D; Fig. 4.16E). At this time plants were longer at sheltered sites than at intermediate sites (Tukey HSD: Sheltered vs. Intermediate, $p<0.05$). For example, plants were c.0.2mm long at sheltered sites and c.0.17mm at

intermediate sites. There was no difference in plant lengths between sheltered and exposed (Tukey HSD: $p>0.05$) or exposed and intermediate (Tukey HSD: $p>0.05$). After 14 days germlings had grown at 0.007mm day^{-1}, slower than in the first 8 days when growth was 0.008mm day^{-1} (Fig. 4.16F).

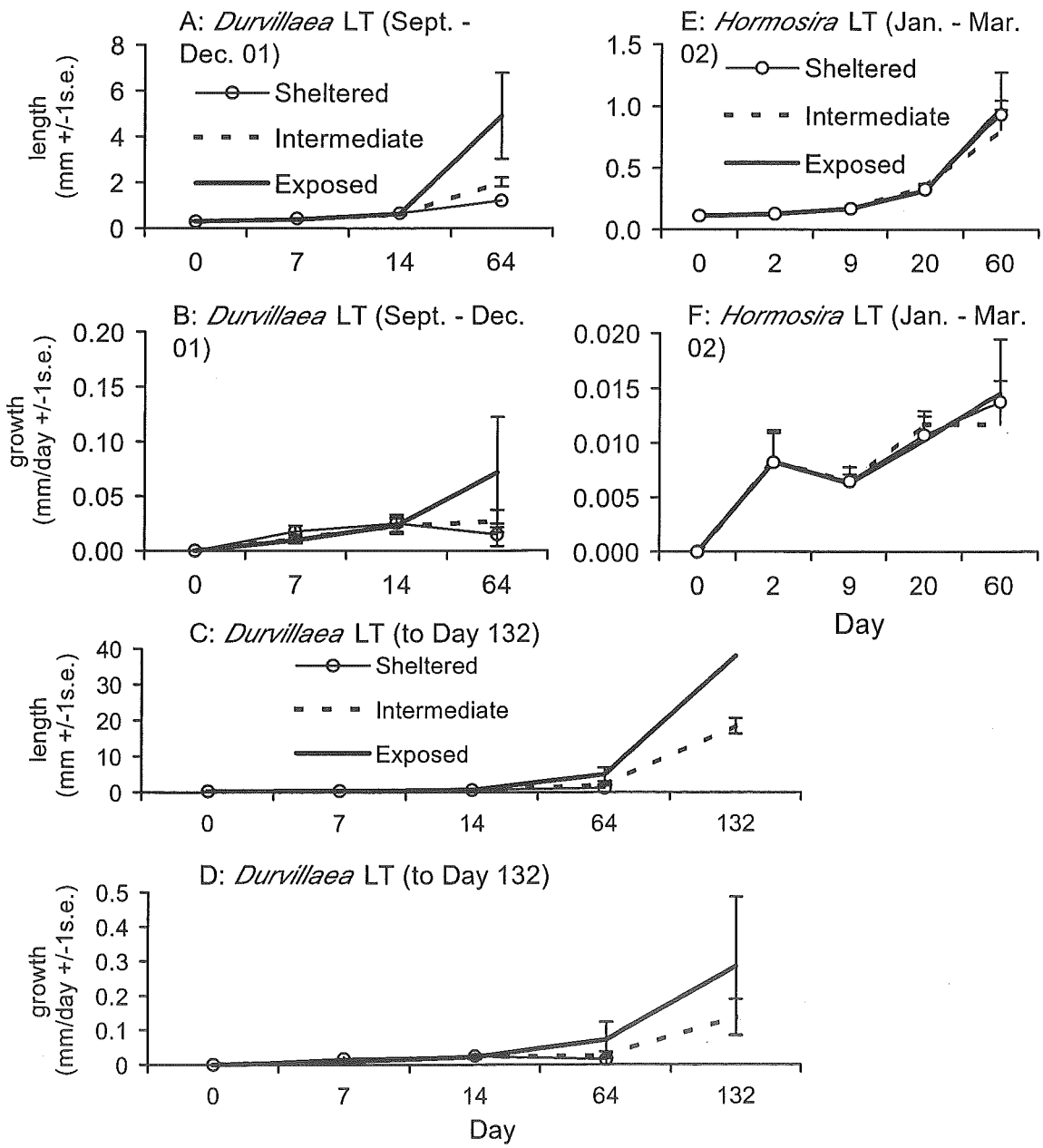

Figure 4.15. Growth and length data from the *Durvillaea antarctica* and *Hormosira banksii* germlings across exposures in LT experiments. NB: C and D are data from the same *Durvillaea* LT experiment monitored up to Day 132.

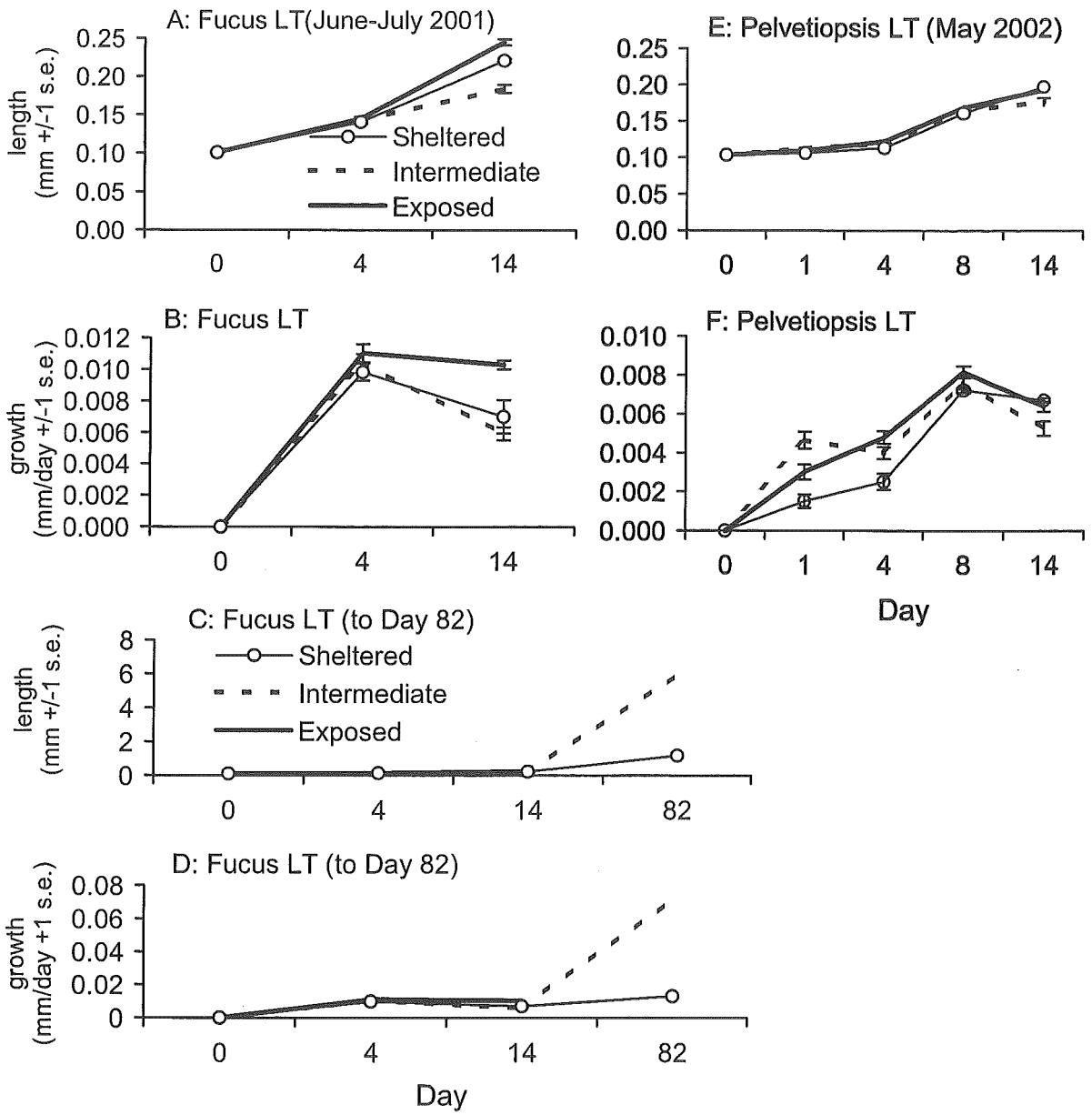

Figure 4.16. Growth and length data of *Fucus gardneri* and *Pelvetiopsis limitata* germlings across exposures in the Oregon LT experiments. NB: C and D are data from the same *Fucus* LT experiment monitored up to Day 82.

Length and growth comparisons across hemispheres

Germlings of *Durvillaea antarctica, Fucus gardneri* and *Pelvetiopsis limitata* after 14 days and *Hormosira banksii* after 20 days had significantly different lengths and different growth rates (Table 4.15A,B; Fig. 4.17A,B). For example, *D. antarctica* was more than three times larger (c. 0.65mm) than *F. gardneri* and *P. limitata* (c.0.2mm) after 14 days. *H. banksii* was monitored at 20 days but was still only half the length of *D. antarctica*. Lengths and growth rates were not significantly different across exposures at this time (Table 4.15A,B)

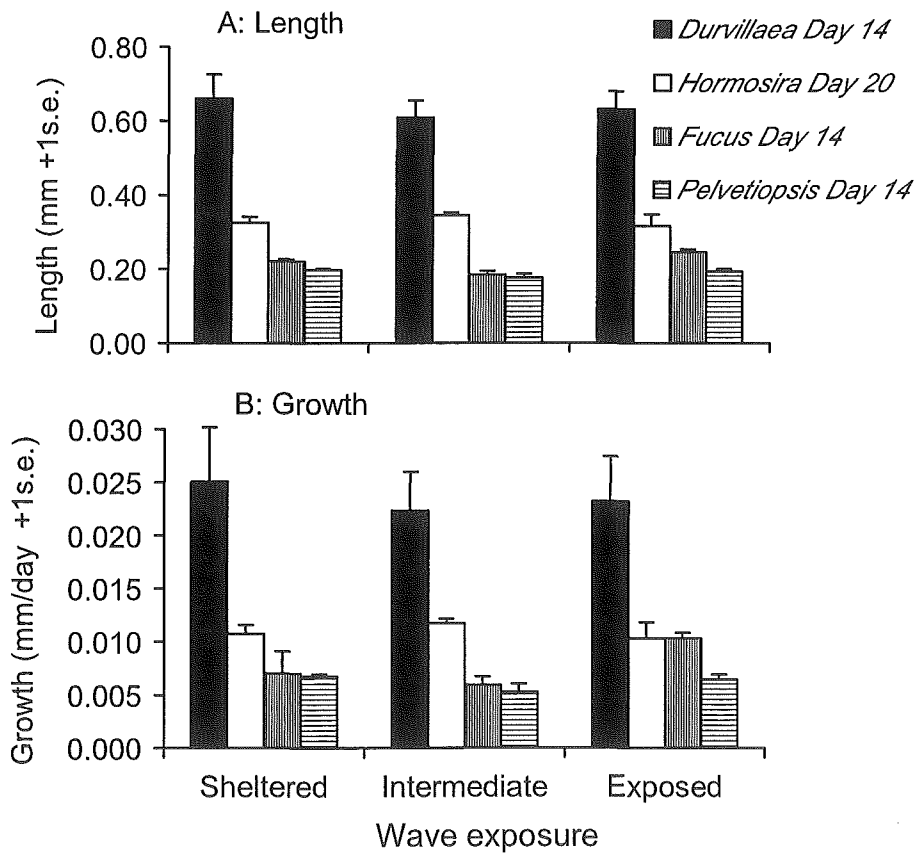

Figure 4.17. Growth and length data of from local-scale transplant experiments at Day 14 for *Durvillaea antarctica, Fucus gardneri* and *Pelvetiopsis limitata* and Day 20 for *Hormosira banksii* germlings across exposures.

Table 4.14. One-way ANOVA results comparing length of A) *Durvillaea antarctica* (Day 14), B) *Hormosira banksii* (Day 20), C) *Fucus gardneri* (Day 14), D) *Pelvetiopsis limitata* (Day 14), E) *Durvillaea antarctica* (Day 64) and F) *Hormosira banksii* (Day 60) germlings across local-scale wave exposure gradients.

A) *Durvillaea antarctica* LT Day 14					B) *Hormosira banksii* LT Day 20			
Effect	df	MS	F	p	df	MS	F	p
Exposure	2	0.010	0.55	0.58	2	0.004	1.44	0.25
Error	33	0.018			47	0.003		
C) *Fucus gardneri* LT Day 14					D) *Pelvetiopsis limitata* LT Day 14			
Effect	df	MS	F	p	df	MS	F	p
Exposure	2	0.004	11.57	<0.001	2	0.0017	4.8	0.02
Error	15	0.001			40	0.0004		
E) *Durvillaea antarctica* LT Day 64					F) *Hormosira banksii* LT Day 60			
Effect	df	MS	F	p	df	MS	F	p
Exposure	2	10.318	5.80	0.02	2	0.063	0.51	0.61
Error	9	1.779			17	0.122		

Table 4.15. ANOVA results for mean lengths at Day 14 for *Durvillaea antarctica, Fucus gardneri and Pelvetiopsis limitata*) and Day 20 *Hormosira banksii* transplanted across local-scale wave exposures. Sites and treatments were lumped within exposures. All Cochrans tests were non-significant.

A) Length				
Factor	df	MS	F-ratio	p
Species	3	1.161	214.20	<0.001
Exposure	2	0.006	1.08	0.34
Species x Exposure	6	0.005	0.95	0.46
Error	135	0.005		
B) Growth				
Factor	df	MS	F-ratio	p
Species	3	0.00177	54.97	<0.001
Exposure	2	0.00002	0.55	0.58
Species x Exposure	6	0.00002	0.60	0.73
Error	135	0.00003		

4.3.8 Grazing effects LT experiments

The effect of grazers on early life stages of large brown algae in experiments repeated in different hemispheres was highly variable but its cumulative effect did not appear to differ across wave exposures.

On the first day after out-planting, there were great differences among the exposures in the grazing effect on *Durvillaea antarctica* germlings (Fig. 18A). There was no grazing effect overall at the sheltered and intermediate sites but 12 percent of germlings were removed by grazers at exposed sites. The negative values at the sheltered and intermediate sites indicate a fence effect because fence control treatments had greater survival than open plates. After 7 days at sheltered and intermediate sites there was still greater survival in fence controls than in open treatments. Between Day 7 and 14, and Day 14 and 64 the grazing effect was 10 percent at sheltered sites and 4 percent at intermediate sites. Negative values at exposed sites indicate higher mortality in fence treatments than in control treatments.

The grazing effect on *Hormosira banksii* germlings was greatest at sheltered sites 2 days after out-planting (Fig. 4.18B). The negative value at the exposed site indicates greater mortality in the fence treatment than control treatments. After 9 days the grazing effect at the sheltered and exposed sites was similar at 30-35 percent. The grazing effect at sheltered sites (35 percent) was twice that of intermediate and exposed sites (15 percent) after 20 days. High mortality in fence treatments across exposures after 60 days reduced the grazing effect to 4 percent at sheltered sites and 1 percent at exposed sites. Negative values at this time indicate greater survival in fence control treatments than fence treatments.

In the *Fucus gardneri* LT experiment similar survival in fence and fence control treatments and greater survival in fence control treatments than in open treatments caused negative grazing effect values (ie. fence effect) at most times and at most exposures (Fig. 4.18C). After 1 day the fence control effect was greatest at intermediate sites at 25 percent. The fence effect was greater at more exposed sites after 7 days but was greater at

sheltered sites after 14 days. Grazing explained 8 percent of *Fucus* germling mortality after 1 day at the sheltered sites and 9 percent at the exposed sites after 4 days.

During the *Pelvetiopsis* LT experiment done in May 2002 the percent of germling mortality attributable to grazing decreased across exposures after 24 hours in the field (Fig. 4.18D). Grazing explained 38 percent of mortality at sheltered sites after one day but this effect declined over time as germling mortality increased within fenced treatments. After 4 days the grazing effect increased across exposures suggesting grazers took longer to have an effect at intermediate and exposed sites. After 8 and 14 days the grazing effect was greatest at the intermediate sites where it was 14 percent.

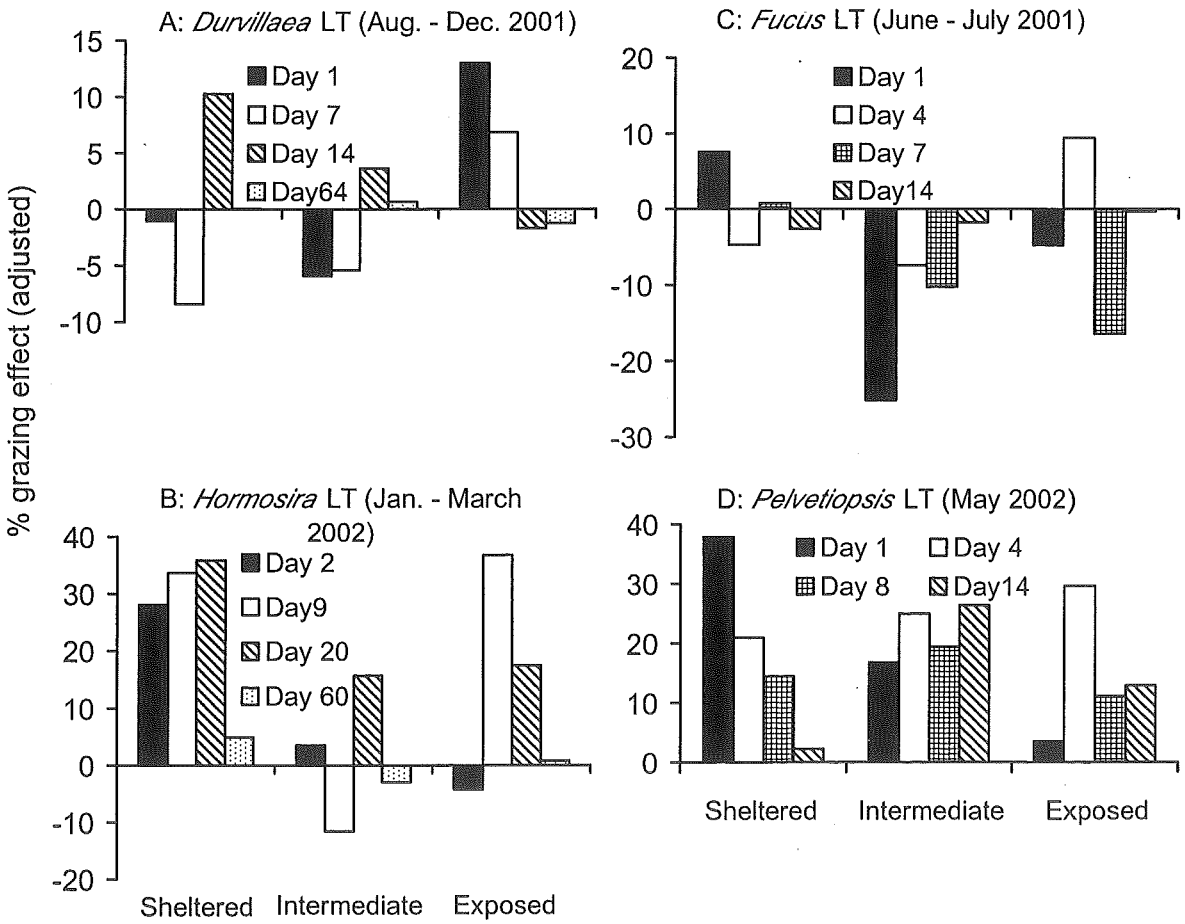

Figure 4.18. Percent of grazing effect (-fence effect) across exposures over time in the A) *Durvillaea antarctica*, B) *Hormosira banksii*, C) *Fucus gardneri* and D) *Pelvetiopsis limitata* LT experiments.

4.3.9 Grazer abundance in Kaikoura LT experiments

Sampling in five 1m long cracks at First Bay and Seal Reef on Kaikoura peninsula showed the abundance of invertebrate grazers decreased as exposure increased with up to 38 per m at the sheltered Seal Reef site and < 1 per m at the exposed Seal Reef site (Fig. 4.19A). The opposite trend was found for grazers on flat rock with greater numbers of grazers found at exposed sites than at intermediate and sheltered sites (Fig. 4.19B). The most common grazers at both sites were the large turbinid gastropod *Turbo smaragdus* and limpets *Patelloida* species.

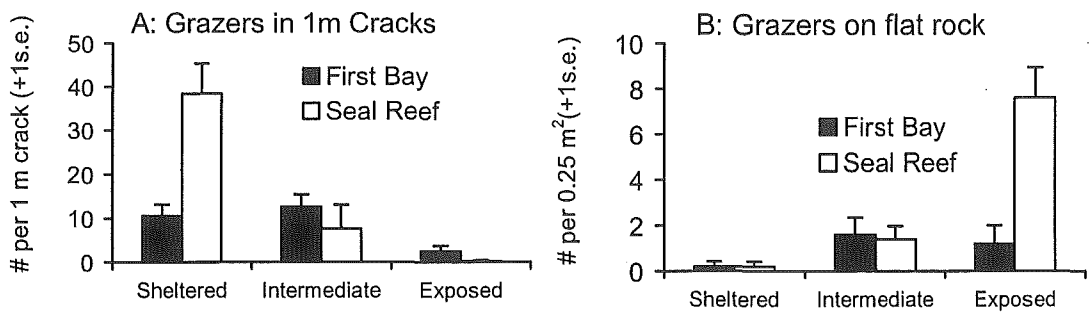

Figure 4.19. Total abundance of invertebrate grazers in 1m cracks (A) and in 0.25m^2 quadrats (B) at sites across exposures used in the Kaikoura LT experiments.

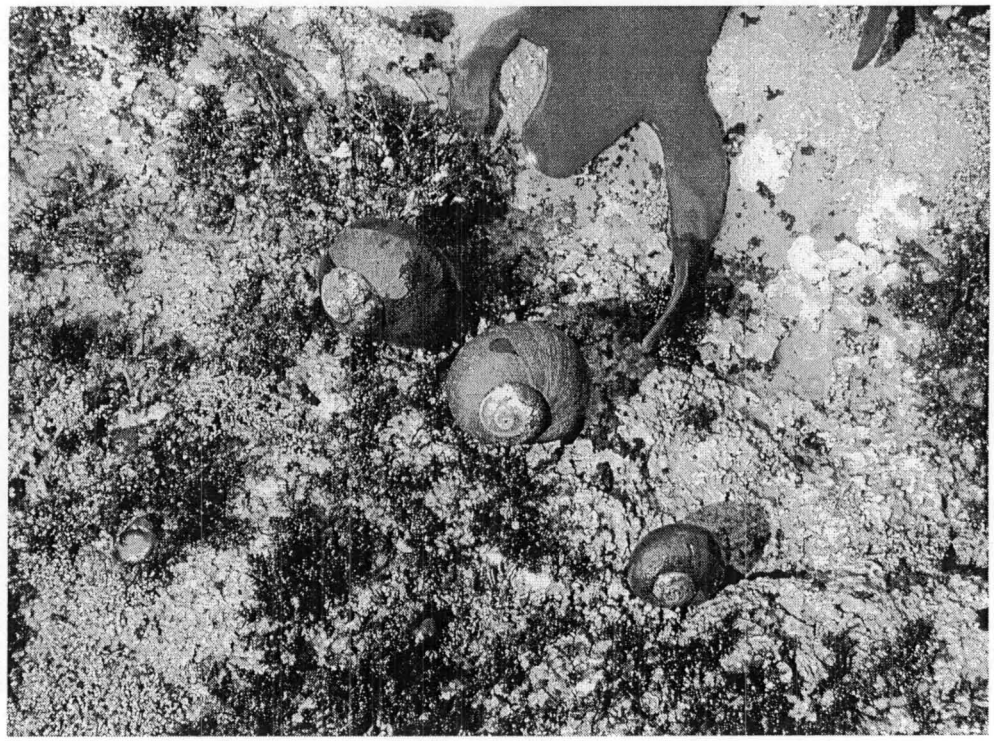

Figure 4.20. The ubiquitous *Turbo smaragdus* (15-40mm long) in the lower intertidal at Kaikoura.

4.3.10 Grazer abundance in Oregon LT experiments

The abundance of grazers was monitored on flat rock in five 0.25m^2 quadrats in June 2001 and May 2002 in Oregon. Compared to New Zealand sites, very large numbers of small limpet and littorinid grazers were present in the lower tidal zone across exposures. At both times total grazer abundance varied significantly between sites within exposures (Table 4.16A,B) but not across wave exposures. For example, in 2001 Topshells, mainly *Littorina scutulata* and *Tegula funebralis*, were more abundant at the sheltered and intermediate sites at Fogarty Creek reaching densities of c. 300 per 0.25m^2 (Fig. 4.22B). Small limpets (*Lottia* species) were abundant at intermediate and exposed sites at Depoe Bay and Fogarty Creek reaching up to 250 per 0.25m^2 (Fig. 4.22A, C). In May 2002 limpets were most abundant at the sheltered Depoe Bay site and the intermediate Fogarty creek site at densities of 125 and 200 per 0.25m^2 respectively (Fig. 4.22B). Topshells, mainly *Littorina scutulata*, were most abundant at the intermediate Fogarty Creek site in May 2002 at densities of c 110 per 0.25m^2.

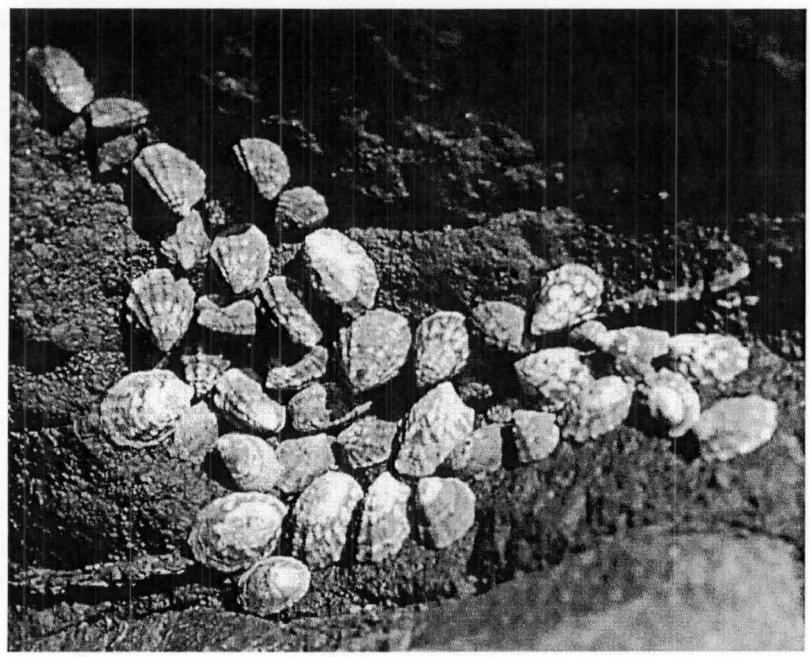

Photo: Patti Halpin

Figure 4.21. *Lottia digitalis* (10-15mm long) abundant at both Oregon sites.

Table 4.16. ANOVA results of invertebrate grazer abundance per 0.25m^2 in A) June 2001 and B) May 2002 on open substratum at Fogarty creek and Depoe Bay, Oregon, testing the effects of Wave Exposure and Sites. Sites were treated as random and nested in exposures. Cochrans tests were not significant.

Factor	df	MS	F	p
A) June 2001				
Exposure	2	124210.0	1.04	0.455
Sites (Exp)	3	119736.0	11.32	<0.001
Residual	24	10569.6		
B) May 2002				
Exposure	2	31149.30	0.41	0.697
Sites (Exp)	3	76167.66	8.39	<0.001
Residual	24	9079.97		

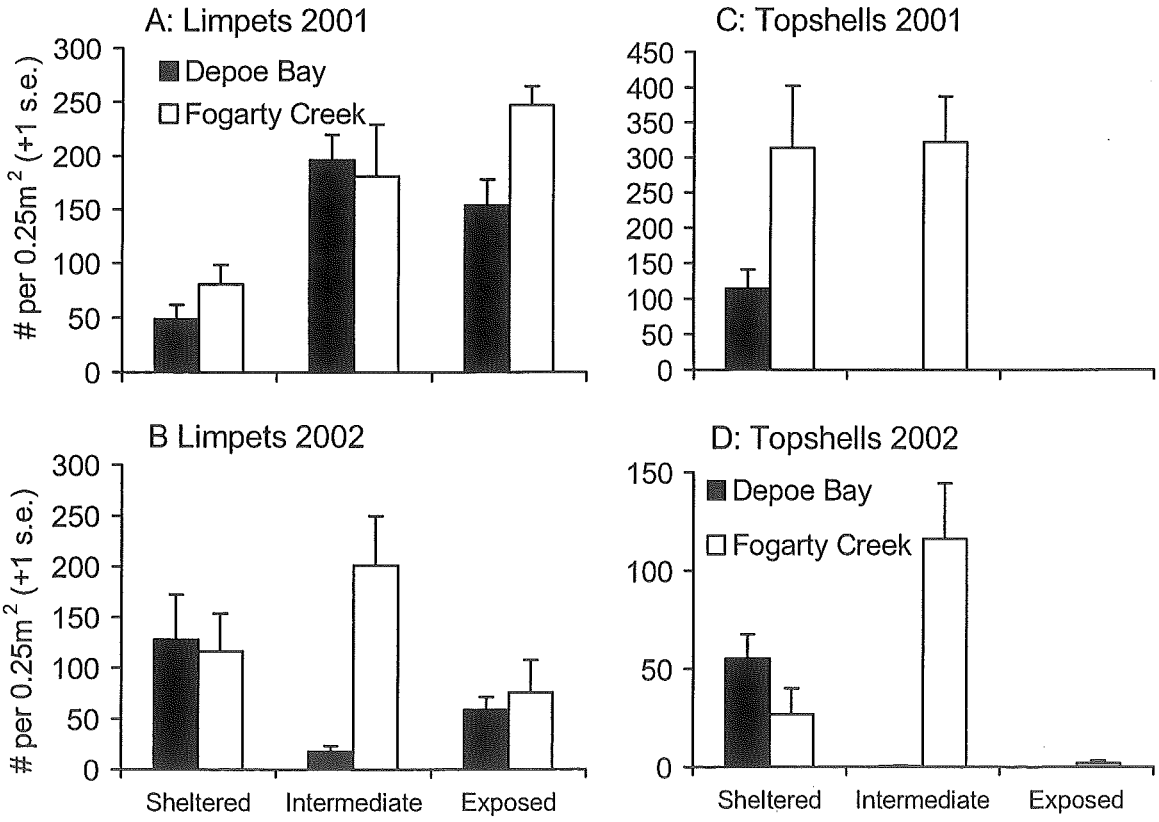

Figure 4.22. Abundance of Limpets (*Lottia* species) and Topshells (mainly *Littorina scutulata*) in 0.25m^2 quadrats across exposures at Depoe Bay and Fogarty creek Oregon in June 2001 (A, C) and May 2002 (B, D).

4.3.11 Wave climate

Dynamometer data confirmed the classification of sites in each wave exposure category for all regional experiments (Fig. 4.23A-D). However, data also indicate during winter months intermediate sites can experience similar maximum wave force recordings to exposed sites, as in June 1999 (Fig.4.23C). During the LT experiments wave forces confirmed site allocation at most times (Fig 4.24A-D). However, variable wave force was at sheltered and intermediate sites in the Pelvetiopsis LT experiment during May -Jun 2002 when lowest levels of wave force were recorded at the intermediate Fogarty Creek site (Fig. 4.24D).

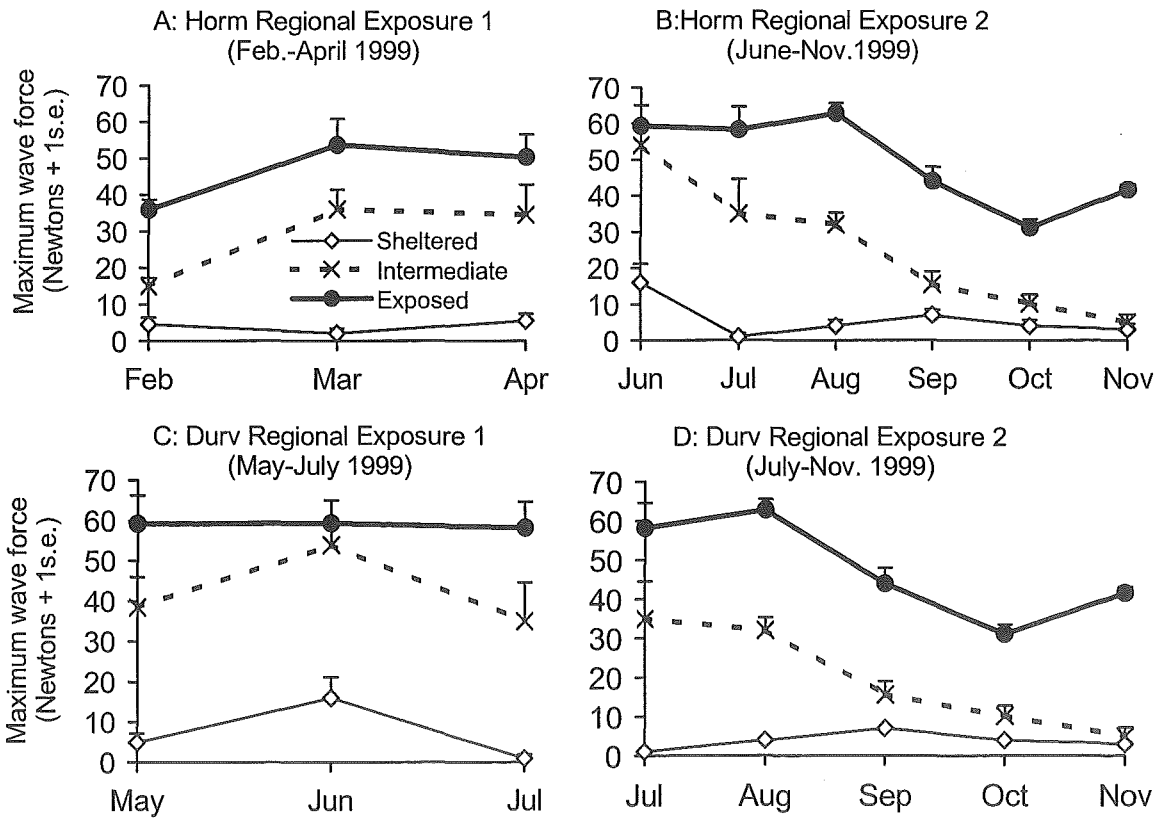

Figure 4.23. Maximum wave force recordings from dynamometers (n=3 per site) across the wave exposure gradients used in the RT experiments. Data from sites within each exposure are grouped.

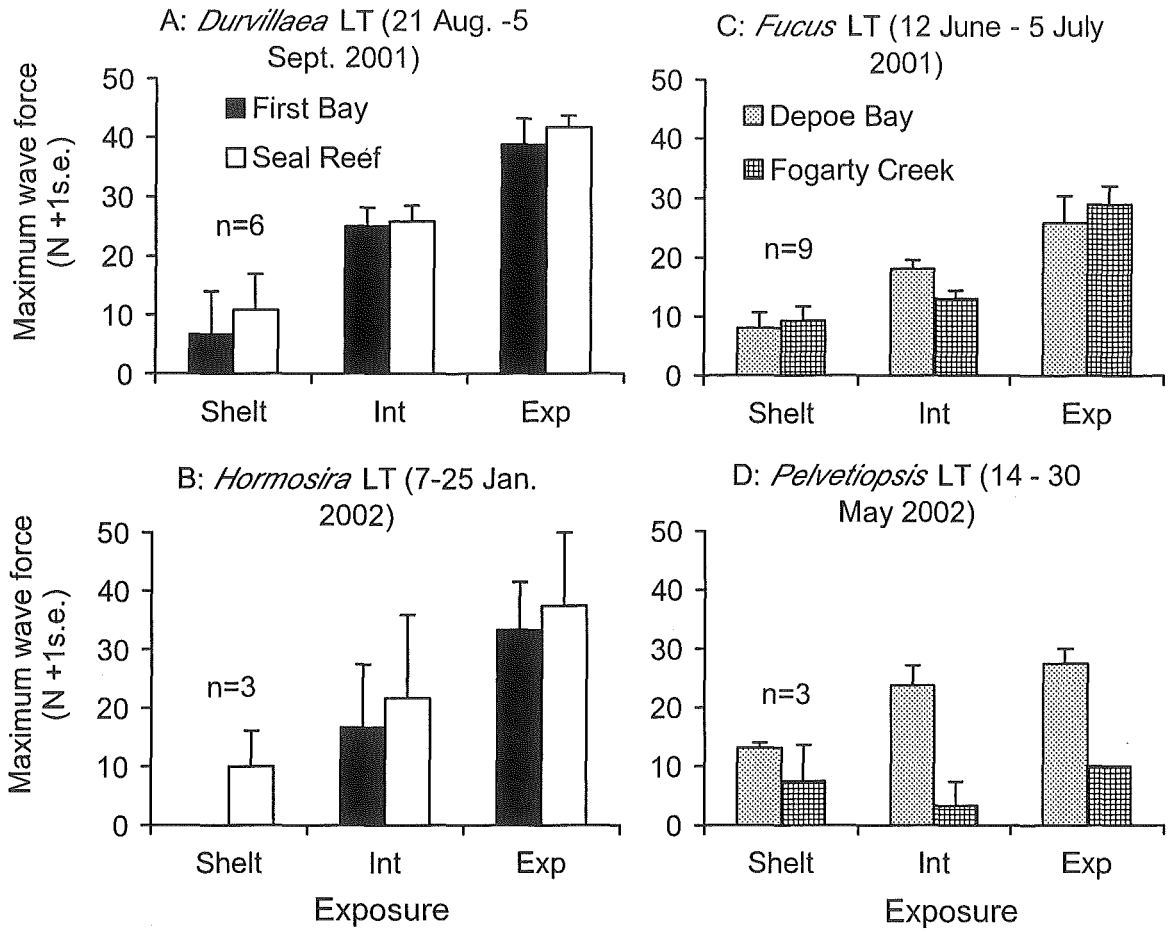

Figure 4.24. Maximum wave force recordings from dynamometers across wave exposure gradients used in the LT experiments in New Zealand (A, B) and Oregon (C, D).

4.3.12 Ephemerals and Sedimentation

Figure 4.25 shows the average percent cover of ephemerals and sediment lumped from all treatments and all times in regional and local-scale transplant experiments. Ephemeral algae settled into all treatments in all experiments, particularly where grazer had been excluded. Sediment settled out at sheltered and intermediate sites in most experiments. Sand was most abundant at the sheltered Fogarty Creek site and the intermediate sites in New Zealand.

RT experiments

In all RT experiments sediment occurred at sheltered and intermediate sites (Fig. 4.25A). In all four RT experiments the greatest cover of sediment was found at sheltered sites. Sediment at sheltered sites was fine silt but at intermediate site most sediment was coarse sand. In contrast, ephemeral algae grew to the greatest cover at exposed sites in all RT experiments (Fig. 4.25B).

LT experiments

In all LT experiments the greatest percent cover of sediment was recorded at sheltered sites (Fig. 4.25C). More sediment occurred in New Zealand LT experiments than in Oregon experiments. Ephemeral algae grew to the greatest cover at the intermediate sites in the *Durvillaea* LT experiment but were most abundant at the exposed sites in the *Hormosira* LT experiment (Fig. 4.25D). In Oregon ephemeral algae, particularly benthic diatoms, had the greatest cover at exposed sites the 2001 *Fucus* experiment but were similar in percent cover across exposures in the *Pelvetiopsis* LT 2002 experiment

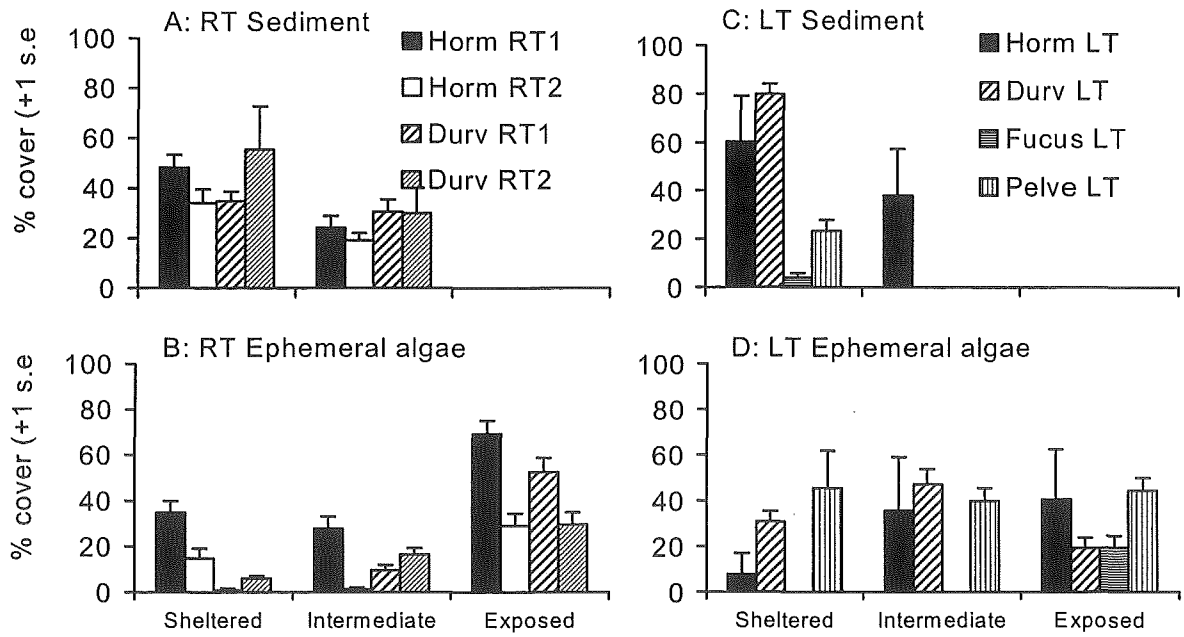

Figure 4.25. Percent cover of sediment and ephemeral algae in all regional and local scale transplant experiments across wave exposures (Sites and treatments lumped).

4.4 Discussion

Mortality of germlings transplanted across wave exposures was invariably greatest immediately after out-planting. This suggests two things. First, that the initial 2 weeks following settlement can represent a bottleneck for early life stages of algae, and second, that the effects of grazers are highly variable.

Early life stages are a bottleneck for many marine algal populations (Pollock, 1969; Allen, 1977; Lubchenco, 1983; Reed, 1990; Brawley and Johnson, 1991; Vadas et al. 1992; Reed, 2000). Vadas et al. (1992) list six intrinsic and 17 extrinsic factors that have been shown to affect algal recruitment from microscopic early life stages to larger recruit stages. Intrinsic factors included relative spore viability, attachment capabilities, growth rates and size. Extrinsic factors included the affects of environmental factors like sediments, substrate, water motion and temperature and biological factors like inter/intra specific competition, canopy effects and grazing.

Historically, intertidal ecologists have used transplant experiments to test factors that affect the competitive abilities, vertical distributions and morphologies of algae by measuring growth rates and physiological tolerances. For example, Pollock (1969) transplanted both embryos and mature *Fucus* plants across tidal zones at Friday Harbour, Washington and found differences in morphology occurred at later stages and were not a result of selective pressure. Schoenbeck and Norton (1980) monitored naturally settled *Pelvetia canaliculata* and *Ascophyllum nodosum* within cleared *Fucus spiralis* canopies across tidal zones in Scotland and found that grazer effects and life history differences determined early life stage survival. In a more recent study, Chapman and Johnson (1990), used adult and juvenile (germling) transplants across tidal zones to investigate the roles of physiological tolerances, and interactions with other organisms in determining the zonation of four *Fucus* species in Nova Scotia. Their results indicated that the physiological tolerances of the component species explained only a small part of the patterns of distribution and suggested other factors like competition and grazing were important. Surprisingly, although suggested by Chapman and Johnson (1990), few studies

have investigated the factors affecting the distribution and abundance of early life-stages of algae horizontally along intertidal shores (Foster, 1990; Hurd 2000).

Transplanting early life stages of habitat-forming algae horizontally along intertidal shores is essential in order to understand the micro-scale environmental and biological processes determining their distribution and abundance at larger scales. However, due to changes in rock type, aspect and habitat it is difficult to standardise sites and control for all variables. In my study, I used a standard substratum and attempted to control for as many variables as possible. Consequently, my controlled transplants allowed comparisons of physiological tolerances and growth rates and enabled tests of the relative vulnerabilities of these algae to grazing of species across hemispheres. I found that mortality of early post-settlement stages of algae across exposures in Oregon and New Zealand was approximately 95 percent for all species within the first two weeks and in most cases only a small percentage of this mortality could be attributed to grazing. Other studies have found similar although variable survival rates (Schiel, 1981; Reed, 1990b; Vadas et al. 1992; Kendrick and Walker, 1994). For example, Kendrick and Walker (1994) found that 99.98% of *Sargassum* spp. embryos died within 2 months of the end of the reproductive season.

High mortality of early post-settlement stages has important consequences for algal populations, affecting inter and intra-specific interactions, the subsequent recruitment to larger size classes and the influence of extrinsic biological and environmental factors (Foster, 1975a,b; Schiel, 1981; Reed, 1990b; Vadas et al. 1992). However, in many cases the specific causes of high mortality at early life stages remain unknown and untested (Chapman, 1984; Vadas et al., 1992). In this study, at most times, the percent survival of germlings of *Hormosira* and *Durvillaea*, and *Pelvetiopsis* and *Fucus* was highly variable and was not significantly different across exposures. There are several explanations for variable survival within and between sites and experiments. For example, differences in wave action, temperature and desiccation stress during each experimental period can be important. Experiments done during winter months

experienced greater wave action, lower average temperatures and shorter daylight hours. Furthermore, the timing of transplant experiments in relation to tidal elevation fluctuations may also have attributed to high mortality within the first few weeks. Most experiments were started at the beginning of low-tide series during which higher temperature ranges were recorded. The combined effects of low tide coinciding with hot weather are known to lead to high mortality in early life-stages of algae. For example, Brawley and Johnson (1991) found that almost all germlings of *Pelvetia fastigiata* died when transplanted outside adult canopies after 1 day. Using an agarose bead method, Brawley and Johnson (1993) found zygote survival was highest in damp sites and also that temperature alone was often not a good predictor of desiccation. Their studies suggest variations in dampness can be caused by the microhabitats formed by turfing species and the micro-topography of the shore. Laboratory and field based studies have also found desiccation stress and water temperature to affect rhizoid development (Wright and Reed, 1990; Davison et al., 1993) and growth (McLachlan, 1974; Fletcher and Callow, 1992; Brawley et al., 1999) in several species of *Fucus*. It is likely that the low survival rate in the *Fucus* local transplant experiment in my study was due to the desiccation stress caused by hot days and very low tides during June 2001 in Oregon.

4.4.1 Growth rates

The growth rate of early post-settlement stages of algae determines the amount of time they are exposed to the negative effects of factors like abrasion, grazing and inter-specific competition associated with microscopic size (Underwood, 1985). Two studies on adult stages of algae found differences in growth rates and annual production across gradients of wave exposure (eg. Gerard and Mann, 1979; Sjøtun et al., 1998) but no studies have tested this effect on very early life stages (Hurd, 2000). In this study, due to different reproductive periods and logistical constraints, experiments on each species were done at different times. However, growth rates were consistently higher when experiments were done outside winter months and were significantly different for species

used in the local scale transplant experiments. For example, *Durvillaea antarctica* had twice the growth rate of all other species during the first 14 days of the local-scale transplant experiments.

The most commonly cited extrinsic variables shown to affect the growth of early post settlement stages of algae are light, temperature and nutrients (Vadas et al., 1992). All three variables interact and when the right combination of the three converge with favourable biological conditions, "recruitment windows" occur (Dayton and Tegner, 1984; Deysher and Dean, 1986). Recently, field studies in Germany have shown nutrient additions can affect not only the growth rates of ephemeral algal species but also the composition of ephemeral algal communities (Lotze et al., 2001). However, the addition of nutrients has rarely been found to benefit fucoid algae. For example, Lotze et al. (2001) found the growth rate of *Fucus* in Germany was not affected by nutrient addition. Furthermore, Lotze et al. (2000) suggest the reduction in *Fucus* abundance in Germany's water ways is due to the negative effects of epiphytic algae on *Fucus* caused by anthropomorphic eutrophication. Australian laboratory studies by Doblin and Clayton (1995) and Bellgrove et al. (1997) found that high concentrations of nutrients reduced germination and growth of *Hormosira banksii.* The neutral or negative nutrient effect on fucoid algae is not universal Van Alstyne and Pelletreau (2000) found nitrogen addition increased growth rates of *Fucus gardneri* embryos in culture.

In my study, growth rates of post-settlement stages were also affected by wave exposure. In most cases the algal germlings grew better at wave exposed sites and often had poorest growth at sites of intermediate exposure. Several hypotheses can be postulated for greater growth at exposed sites. Most are related to interactions between temperature, water flow, turbulence and nutrient transfer across boundary layers but few can be tested directly in the field because of the microscopic scale at which these interactions take place (Stevens and Hurd, 1997; Hurd, 2000). The water surrounding propagules (i.e., about the first 1mm of water) is distinct from the water above in that it does not move relative to the substratum, known as the "no-slip condition" (cf. Vogel,

1981; Denny, 1987a,b). The gradient from the free flowing water above to the motionless water at the substratum is known as the 'benthic boundary layer'. This condition creates unique problems for microscopic germlings in acquiring the nutrients required for growth. Turbulence can increase nutrient transfer (Hurd et al., 1996). The ratio of inertial to viscous forces or Reynolds number, *Re*, is an indicator of whether a benthic organism will experience turbulent or laminar flows (Hurd, 2000). Turbulence usually occurs in the upper part of the boundary layer through breaking waves and decreases towards the bottom (Vogel, 1987), but it also begins at the substratum and moves up, generated by substratum roughness (Denny, 1987). In the intertidal zone it can take flows of less than 1m sec^{-1} to create a turbulent boundary layer (Denny and Shibata, 1989). These are flows not unusual in the intertidal zone, even on sheltered shores. For example, during the first 2 days of the *Durvillaea* LT experiment velocities of up to 2.5 metres sec^{-1} were recorded high on the shore between the Seal Reef and First Bay sites (Geography Department, 2002). It is possible, therefore, that increased turbulence at exposed sites could, therefore, increase nutrient transfer across boundary layers and increase growth. However, the effects of water motion on macroalgal production have been shown to be variable and few studies have looked at early life-stages (Hurd, 2000). Studies by Gerard and Mann (1979) and Sjotun et al. (1998) measured macroalgae production *in situ* as a function of water motion. Both studies were on *Laminaria* species and both found variable results of either negative, positive or no correlation of production across wave exposures depending on species, age of plants and sites. In New Zealand, however, South and Hay (1979) found a positive relationship with the density and standing crop of *Durvillaea antarctica* and wave exposure. My results indicate early life stages of large brown algae are not physiologically stressed by greater wave action associated with wave exposed sites and may in fact benefit from increased nutrient transfer across benthic boundary layers.

An interesting feature of these experiments was that survival and growth of all algae was poorest at intermediate sites. At first this result appears counter-intuitive

because in New Zealand that is where large brown fucoid algae, especially *Hormosira banksii* and *Cystophora torulosa,* dominate the mid and lower tidal zones respectively. A possible explanation is that factors like sand scour, slower growth and interactions with grazers and other algae had a cumulative effect and tipped the balance at intermediate sites. Another explanation could relate to the substratum used in this study. The plates probably afforded little protection from sand scour and desiccation at intermediate sites. The algae that dominate at these sites are often seen recruiting into low coralline turfs or barnacle tests. The microhabitat they provide could protect germlings from desiccation, sand scour and grazing effects and may be required by the early life stages of algae like *H.banksii, C. torulosa, Fucus gardneri* and *Pelvetiopsis limitata* to recruit successfully.

4.4.2 Ephemeral algae

One factor that is consistent with higher nutrient availability at exposed sites in this study was the faster growth and greater cover of ephemeral algae in grazer exclusion treatments at exposed sites. Ephemerals have been shown to be particularly sensitive to nutrient addition and increased nutrient loads have resulted in blooms of ephemerals in many eutrophic coastal ecosystems (Lotze and Worm, 2000). Both brown and green ephemeral diatoms and foliose algae like *Ulva lactuta, Scytospihon* sp., *Colpomenia peregrina, Adenocystis* and *Enteromorpha* species are often found only at intermediate sites but settled across all exposures in all treatments in New Zealand, particularly those fenced from grazers.

Ephemeral diatoms and foliose algae in my study appeared to out-compete and/or epiphytise germlings in grazer exclusion treatments (Pers. obs). I saw plants in Oregon and New Zealand effectively smothered by a complex of ephemeral algae and diatoms. Although no specific test of this effect was done, negative effects of ephemerals on perennial algae survival and recruitment have been found in several studies. For example, Lotze et al. 2000 describe a reduction in *Fucus* habitat as adults were epiphytised after eutrophication of German waterways. Sousa (1979a,b) showed that ephemeral algae,

mainly *Ulva lactuta*, slowed succession in the intertidal boulder fields of Santa Barbara. Lubchenco (1983) found similar results on New England shores, where *Littorina littorea* sped up succession by removing ephemeral species. However, Menge et al. (1993) found variable effects of ephemerals at different wave exposures in the low-shore on the central Oregon coast. At exposed sites they found ephemerals had no effect on the recruitment of *Constantinea simplex* and at one sheltered site they were found to negatively affected recruitment of *Odonthalia* but not at the other. Further study of the effects ephemeral algae on the growth and survival of early life stages of perennial algae across gradients in wave exposure is required.

4.4.3 Sedimentation

Sedimentation is a consequence of low flow rates and was also associated with lower survival in the current study. Sediments were observed at all sheltered and intermediate sites often covering the surrounding geniculate coralline algae beds. In my study, coarse sand sediments at the intermediate sites in New Zealand and the sheltered sites in Oregon may have contributed to poor growth and survival of all species through a combination of abrasion and smothering. In a separate study, Schiel et al. (In press) found the inclusion of grazers resulted in a reduction of the cover of sediment in treatments, suggesting grazers may indirectly affect germling survival by preventing accumulation of sediments on flat surfaces.

Sedimentation has been observed in several intertidal and subtidal studies and its effects on the growth and survival of algae have been documented. For example, Foster (1975b) found sediment to be a significant factor in the growth and survival of *Macrocystis pyrifera* sporophytes in California kelp forests. Devinny and Volse (1978) showed the attachment and survival of cultured *M. pyrifera* was reduced by as little as 8mg cm^{-2} of fine sediment less than 74 μm in size. However, sedimentation effects on algal survival are not always negative. For example, sand inundation facilitated survival of perennial macroalgae but inhibited recruitment of opportunistic algal species on San Nicolas Island,

California (Taylor and Littler, 1982). In another study, both the structure and diversity of algal assemblages on a rocky subtidal site in the Mediterranean were affected by variation in sedimentation rates depending on the successional period in which it occurred, the species life history characteristics and indirect effects mediated by competitive outcomes (Airoldi and Cinelli, 1997). Although I removed algal canopies immediately surrounding experimental areas, other studies have found macroalgae can mediate the movement of water and affect the surrounding sediment dynamics. In their review, Madsen et al. (2001) found macrophyte beds reduced water velocity, increased sedimentation and determined particle size of sediments. I observed that sand scour reduced survival of early-life stages of perennial algae across wave exposure gradients particularly at intermediate exposures in New Zealand and at the sheltered sites in Oregon. Small amounts of fine sediments may have facilitated survival at sheltered sites in New Zealand by reducing desiccation stress. Furthermore, grazers appear to have the indirect effect of aiding the re-suspension of sediments.

4.4.3 Grazing across hemispheres

I specifically tested the model that invertebrate grazer effects would decline at greater wave exposures in different hemispheres. In experiments in New Zealand and Oregon the effect of grazing on germling survival was small compared to the high percentage of unexplained mortality. In fact, in most cases the effect of grazing was more one of 'mopping -up' the germlings that remained in the open and control treatments. The mopping-up effect was similar across exposures in all experiments as the fairly homogeneous plates used in this study provided little refuge from grazers.

In Oregon large numbers of limpets (*Lottia* species) were observed grazing on plates across all levels of wave exposure. In New Zealand, *Turbo smaragdus* at sheltered and intermediate sites and the cryptic *Chiton pelliserpentis* and suites of limpets at the exposed sites were effective at removing the remaining germlings from plates. Consequently, the model that grazing effects would decline at greater exposures was not

supported. Other studies have found similar results when testing the effects of grazers on algal communities because some grazers, particularly limpets and chitons, function successfully in high stress environments. For example, Cubit (1984) found limpet grazing efficiency on the intertidal shores of Oregon did not decline during harsher winter conditions and found instead that grazing rates remained constant and algal growth rates increased during over the winter period to the extent that they outgrew grazer effects. Kim (1997), also found limpet grazers increased the rate of algal succession by removing ephemerals despite strong desiccation and a harsh wave climate on the upper shore in British Columbia. Both studies conclude that grazing effects are equally strong in high stress and harsh environments and that algal growth rates and surface heterogeneity ultimately determine algal distribution and abundance in exposed conditions. My results indicate that over time invertebrate grazing is equally important in determining the survival of early life stages of these habitat-forming algae at all levels of wave exposure but greater growth at exposed sites may provide a mechanism for algae to escape through size.

In my study, invertebrate grazers initially directly affected survival of germlings by consuming them but later appeared to indirectly affect germling survival by moving sediments and reducing the ephemeral algae and diatom cover. Several studies have found invertebrate grazers to influence intertidal community structure by consuming ephemeral algae. For example, Lubchenco (1978) found that on the emergent areas of intertidal shores in New England algal diversity was negatively affected by grazing and up to 14 species of ephemeral algae coexisted with perennial algae if grazers were removed. In a more recent study, Kim (1997) found limpets in the upper tidal zone of Oregon intertidal shores sped up succession by removing ephemerals allowing perennial algae such as *Fucus gardneri* and *Pelvetiopsis limitata* to recruit into a barnacle dominated habitat. In contrast, Jenkins et al. (1999) found limpet grazers in the low shore slowed succession and recovery by consuming the dominant alga *Fucus serratus* on the Isle of Mann. The interaction between grazers and microalgae is, therefore, complex and their

indirect positive effects on the early life stages of these algae by preventing sediment accumulation (as per Schiel et al. In review) and ephemeral cover may be as important as the direct affects of germling consumption and therefore merits further examination.

4.4.4 Summary

To my knowledge this is the first study detailing differences in growth and survival of early post-settlement stages of perennial algae across wave exposure gradients in different hemispheres. Because all algae survived and grew to visible recruits at exposures outside where they are naturally most abundant my results suggest that the post-settlement to recruitment phase is not limiting for habitat-forming brown algae across exposures in either hemisphere. My experiments also critically tested the model that grazing on germlings of habitat-forming algae would be less effective at greater wave exposures. No evidence was found for a decline in grazer effects but interactions with ephemeral algae and sediments were important at different exposures.

Sand-scour appeared to have a major effect on germling survival. Consequently, patterns of survival on the experimental substratum was often in contrast to the natural distributions of algae. For example, *Hormosira banksii, Fucus gardneri* and *Pelvetiopsis limitata* are most abundant at sheltered and intermediate exposures. In general, *H. banksii* had greater survival and growth at sheltered and exposed sites, and *F. gardneri* and *P. limitata* had greatest survival at intermediate and exposed sites where sand was not present. Furthermore, the exposed shore species *Durvillaea antarctica* often had greater survival at sheltered and exposed sites but poorer survival at intermediate sites where sand was abundant. Interactions with barnacles, for *P. limitata* and *F. gardneri*, and turfing coralline algae, for *H. banksii* probably provide the mechanism that allows escape from sand scour effect in natural environments. Ultimately, size and holdfast attachment strength become factors in the distribution of species such as *P. limitata*, *F. gardneri* and *H. banksii* across exposures (Gaines and Denny, 1993; Blanchette, 1997). However, because of its great attachment strength and flexibility alternative hypotheses must be

postulated to explain the distribution of *D. antarctica*. For example, *D. antarctica* may be unable to recruit into turfing coralline algae and is, therefore, exposed to grazing on the open substratum. Alternatively, there are different processes acting on recruit stages in sheltered conditions. These hypotheses are visited in Chapter 5.

Chapter 5

RECRUITMENT OF *DURVILLAEA ANTARCTICA*: A HABITAT-FORMING ALGA

Grazing, canopy and substratum effects

5.1 Introduction

For many species of foliose algae, exponential growth after recruitment leads to a size and toughness refuge from invertebrate grazers (Santelices, 1990b; Chapman, 1995). However, each life stage is exposed to a new suite of challenges that determine its ability to survive, grow and establish or replace adult populations. The probability of germlings surviving through the milieu of biological and environmental variables associated with the benthic boundary layer to become visible recruits is extremely low (Vadas et al. 1992; Amsler et al. 1992).

The major habitat-former and biomass contributor in the lower tidal zone along much of New Zealand's exposed coastline is the bull kelp, *Durvillaea antarctica* (South and Hay, 1979; Chapter 2). The same species occurs across the southern hemisphere at latitudes between 45-60° S (Hay, 1979b; South and Hay, 1979). It provides habitat for a range of grazing invertebrate species that reside in and around hold-fasts of adult plants (Hay, 1977; Santelices, 1990; Edgar and Burton, 2000). For example, Edgar and Burton (2000) found 23 macro-invertebrate taxa associated with *D. antarctica* holdfasts on the subantarctic, Heard Island. The understorey of *D. antarctica* is dominated by hardy encrusting and turfing coralline algae (Hay, 1977; Santelices, 1990). Once adult *D. antarctica* plants are established only a few species of foliose algae can survive the 'whiplash' effects of plants that can weigh up to 80 kg and be up to 10m long (Santelices et al., 1980).

Across sites of different wave exposures *Durvillaea antarctica* is most abundant at semi-protected and exposed sites but never extends into very sheltered areas (see Chapter 2). At a finer spatial scale I observed recruitment of *D. antarctica* into patches of bare rock created by dislodgement of adult holdfasts by storms. In New Zealand, *Durvillaea antarctica* reproduces during autumn and winter (March-September) and recruits during late winter and early spring (Hay, 1977). I also observed little recruitment on surrounding coralline algae or directly under adult canopies. Similar observations have also been noted for *D. antarctica* populations on the central coast of Chile (Santelices et al., 1980; Santelices and Ojeda, 1984). In central Chile *D. antarctica* recruits year round (Santelices et al., 1980; Santelices, 1990a, b).

Algal canopies can affect spore dispersal, light and nutrient supply to areas below, and the whiplash of fronds and the extensive areas occupied by holdfasts can pre-empt successful recruitment (Dayton et al., 1984; Reed and Foster, 1984; Foster and Schiel, 1987; Kenelly, 1987; Schiel, 1988, 1990; Santelices and Ojeda, 1984; Santelicies, 1990). Consequently, large brown algae often recruit poorly beneath adult canopies compared to gaps outside canopies. For example, Santelices and Ojeda (1984) found that canopy effects and grazing combined to completely inhibit the recruitment of the large brown alga *Lessonia nigrescens* in central Chile. They found that undisturbed areas between holdfasts, provided by dislodgement of adult holdfasts, were required for successful recruitment. They also suggested that outlying adult fronds provided intermittent reduction in grazing pressure. Dayton et al. (1984) examined mechanisms for persistence and resistance of populations of subtidal algae in southern California. They followed demographic patterns of populations over a ten year period and removed canopies and seeded cleared areas with sporogenic material of several algal species. They found a clear dominance hierarchy for light competition determined by adult canopy height but a trade off in the ability of higher canopies to withstand wave stresses. Faster growing laminarians like *Macrocystis pyrifera* were also less resistant to grazing. However, of overriding importance were the life history constraints like dispersal abilities and

growth rates that determined the ability of each species to invade and persist under canopies of other algal species.

The occupation of the substratum by other species can also affect recruitment. Coralline algae, a common feature of the understorey in lower intertidal and sub-tidal habitats, have been found to both inhibit the recruitment of some species and facilitate others. For example, Camus (1994) suggested encrusting coralline algae reduced recruitment of *Lessonia nigrescens* in northern Chile by shedding epithallial cells. In contrast, the favourable micro-habitat provided by turfing corallines has been shown to facilitate recruitment of fucoid algae (Brawley and Johnson, 1991; Bendetti-Cecchi and Cinelli, 1992; Brawely and Johnson, 1993). For example, Brawley and Johnson (1993) found that survival of *Pelvetia fastigiata* zygotes was positively correlated with the microhabitat conditions provided by coralline turfs.

Another common feature of lower intertidal and shallow subtidal zones in temperate areas worldwide is a great abundance of herbivorous gastropods and echinoderms (Hawkins and Hartnoll, 1983; Andrew, 1993). Invertebrate grazers within these zones can have significant impacts on the structure and composition of algal communities (Sousa et al., 1981; Andrew and Underwood, 1989; Jones and Andrew, 1990; Andrew, 1993). For example, along much of the central and northern west coast of USA the purple sea urchin *Strongylocentrotus purpurpratus* dominates the lower intertidal and controls the abundance of both red and brown algal assemblages in this zone (Sousa et al., 1981). Other studies have suggested that the importance of grazing effects in the lower intertidal and shallow subtidal can vary across latitudes (Sousa et al., 1981; Meekan and Choat, 1997; Connolly and Roughgarden, 1998). In New Zealand, the abundance of the urchin *Evechinus choloticus* undergoes a major latitudinal shift. Wherein it dominates large areas of the subtidal in the warmer waters of northern New Zealand, maintaining so called 'urchin barrens', it is less abundant and fails to dominate to the same extent in southern regions (Choat and Schiel, 1982; Schiel, 1990). Latitudinal differences in grazer importance are particularly evident in fish grazers that are more abundant in tropical

environments than in temperate waters (Ebeling and Hixon, 1991; Meekan and Choat, 1997). Meekan and Choat (1997) showed that the relative abundance of herbivorous fish in shallow temperate New Zealand waters was only 20-25% of those at tropical Great barrier reef and Caribbean sites. The most abundant large herbivorous fish in southern New Zealand are the clown fish *Aplodactylus arctidens* and the butterfish *Odax pullus* (Choat and Ayling, 1987; Choat and Clements, 1993; Meekan and Choat, 1997). The prevailing paradigm for the temperate waters of Australasia is that herbivorous fish are generally habitat-followers and of less importance than urchins that can be habitat-formers (Jones and Andrew, 1990).

At the community level, environmental stress models predict that grazers and predators will be less effective at removing prey in high stress environments where physical factors and competition are believed to be more important in controlling community structure (Menge and Sutherland, 1976; Menge and Sutherland, 1987). If applied to exposed shores in southern New Zealand grazers and predators would be predicted to be less important in controlling the distribution and abundance of algae than physical factors. This prediction is in contrast with results of Paine (1974) who found that the abundance of *Durvillaea antarctica* at exposed sites was positively related to the predation effects of the sea star *Stichaster australis*. He found that *Stichaster australis* removed the 'competitive dominant' green-shelled mussel *Perna canaliculus* in northern New Zealand and allowed *Durvillaea antarctica* to recruit successfully. However, this interaction may be less important in other parts of New Zealand. For example, as shown in Chapter 2 *Durvillaea antarctica* is not abundant in the lower tidal zone of very exposed sites on the West coast of the south island. This is surprising because other studies have shown *Stichaster australis* is highly abundant at these sites and the high wave action and frequencies of up-welling events along the west coast should provide ample nutrients for primary productivity (Menge et al., 1999).

Differences in biomass and growth rates of older life-stages of algae across gradients of wave exposure have been found and the absence of *Durvillaea antarctica*

from more sheltered areas may be related to its requirement for nutrient uptake. In Norway, Sjøtun et al. (1998) found that biomass and growth of 4-year-old *Laminaria hyperborea* showed a positive relationship with wave exposure. In contrast, Gerard and Mann (1978) found production of *Laminaria saccharina* was greater at a wave-sheltered sites. There are several possible causes of these differences in growth rates but most relate to water motion and the transfer of nutrients across the blade boundary layer. Several studies have shown that water motion can affect rates of photosynthesis and nutrient uptake in macroalgae (Wheeler, 1980, Leigh et al. 1987; Larned and Atkinson, 1997). Although, other studies have found it difficult to measure the actual environmental and biological factors responsible for patterns of increased algal production at greater water velocities (Hurd, 2000).

There are two main aims of this chapter. First, I test the effects of adult canopies and substratum in controlling the fine-scale distribution and abundance of *Durvillaea antarctica* recruits. Second, I test the effects of herbivory and wave exposure on the growth and survival of recruits. These aims are tested by six hypotheses, I first test: that adult canopies effect the recruitment of *D. antarctica*; that the presence of coralline algae affects recruitment of *D. antarctica;* that, because *D. antarctica* has a discrete reproductive period, the time of substratum removal and canopy clearance will effect the recruitment of *D. antarctica.* Through transplants of recruit stages of *D. antarctica* on plates, I also test the null hypotheses: that the growth of transplanted recruits will be the same across exposures; that the growth of recruits will be the same under, on the edge and outside *D. antarctica* canopies; that the effects of grazing will be the same under, on the edge and outside *D. antarctica* canopies; and that grazing has no effect on the abundance of *D. antarctica* on the west coast of South Island.

5.2 Materials and Methods

The experiments, the study sites and major hypotheses tested in this chapter are summarised in the following table.

Table 5.1. Summary table of experiments, sites, and hypotheses tested relating to the recruitment of *Durvillaea antarctica.*

Experiment	Peninsula	Study sites	Exposure	Hypotheses
Canopy / Substratum	Moeraki	East Reef	Exposed	i) Adult canopy affects recruitment. ii) Substratum affects recruitment. iii) Time of clearance affects recruitment.
	Kaikoura	First Bay	Exposed	
Quadrat Samples	Kaikoura	First Bay	Exposed	iv) The number grazed and the cover of recruits is the same under, outside and on the edge of adult canopies.
		Seal Reef	Exposed	
Recruit Transplants	1) Kaikoura	First Bay	Exposed	v) Recruits growth will be the same across wave exposures.
		Carpark	Intermediate	
	2) Kaikoura	First Bay	Exposed	
		Seal Reef	Exposed	
		Carpark 1	Intermediate	
		Carpark 2	Intermediate	
		Mudstone Bay	Sheltered	
		Jimmy's Beach	Sheltered	
	3)Kaikoura	Jimmy's Beach	Sheltered	
		Carpark	Intermediate	
		Seal Reef	Exposed	
	4) Banks	Devauchelles	Sheltered	
		Caves Bay	Intermediate	
		Boulder Bay	Exposed	
Caged Transplants	1) Kaikoura	First Bay	Exposed	v) Growth will be the same outside and under cages and canopies.
		Seal Reef	Exposed	
	2) Greymouth	Twelve Mile Beach	Exposed	

5.2.1 Study sites

Canopy and substratum clearances

Two algal-covered platforms on the central eastern coast of South Island of New Zealand were used. First Bay, located on the northeastern end of Kaikoura peninsula, is a mudstone platform that extends 70m from the land. At its eroded edge are small fragments of reef covered in *Durvillaea antarctica* (Hay, 1979). Wave action is

greatest at this edge where oceanic swells hit the reef largely unimpeded. The other study site was a platform on the northern end of Moeraki peninsula (see Schiel and Taylor, 1999 for description). It has large beds of *Durvillaea antarctica* on flat but broken reef along its seaward margin.

The species associated with low shore *Durvillaea antarctica* habitat are described in Chapter 2. Main molluscan grazer species are the turbinid *Turbo smaragdus*, chitons *Eudoxochiton nobilis* (Gray), *Onithochiton neglectus (Gray), Amaurochiton glaucus* (Gray), *Chiton pelliserpentis* (Quoy & Gaimard) and *Frembleya egregia* (Adams) and limpets *Patelloida corticata* (Hutton) and *Siphonaria cookiana* (Suter) (in holdfasts). The understorey is dominated by turfing and encrusting corallines like *Haloptilon roseum, Jania* species, *Corallina officinalis* and *Lithothamnion* species. Bare substratum is rare (averaging approx. 5%, see chapter 2) and often only occurs in any abundance where adult holdfasts have detached.

Quadrat sampling

To give some contextual background to the effects of grazing on *Durvillaea antarctica* recruits the number, percent cover and the percent of grazed recruits were assessed in 5 replicate 0.25m^2 quadrats under, on the edge and outside of adult *Durvillaea* canopies at First Bay and Seal Reef sites on Kaikoura peninsula during October 2001.

Recruit transplants

Across exposures

These were initially done between the exposed First Bay site and the intermediately exposed Carpark site on Kaikoura peninsula (see below for methods). A larger scale transplant experiment was then done across wave exposure gradients at two sites within three levels of wave exposure on Kaikoura peninsula. Sheltered sites were Mudstone bay and Jimmy's beach. Intermediate sites were Carpark 1 and Carpark 2 (c.100m apart) and exposed sites were First bay and Seal Reef (Refer to Chapter 1).

Later, recruits were also transplanted across sites of three exposures on both Kaikoura and Banks peninsulas. Kaikoura sites were the sheltered Jimmy's beach site, the intermediate Carpark site and the exposed Seal reef site. The Banks peninsula sites were the exposed Boulder bay site, the intermediate Cave bay site and the sheltered Devauchelles site. At all sites algal canopies were removed from experimental areas.

West Coast transplants

Durvillaea antarctica recruits from the First bay site in Kaikoura were also transplanted to Twelve mile beach, an exposed site 12 miles (20 km) north of Greymouth west coast of the south island. This was done to test if fish grazing was as important in determining the abundance of *Durvillaea antarctica* on the West Coast.

Caging experiments

To test the effects of fish grazing, recruits were also transplanted into and outside cages under, on the edge and outside of *Durvillaea antarctica* canopies at Seal Reef, and outside *D. antarctica* canopies at First Bay, Kaikoura and Twelve mile beach, Greymouth.

5.2.2 Experimental Design

Canopy and substratum clearances

To test the effects of canopy, coralline algae and time of disturbance on the recruitment of *Durvillaea antaractica* four treatments were used; +Canopy +Coralline algae, +Canopy -Coralline algae, -Canopy +Coralline algae, -Canopy -Coralline algae (Table 5.2). 30 x 30 cm plots were marked under a canopy or in an area where the canopy had been cleared and randomly assigned as plus or minus coralline algae. Plots were marked with a plastic anchor plug (Ramset 6mm). The coralline algae removal treatments were scraped back to bare rock using a tile hammer. There were four

replicates of each treatment. To test the effect of platforms the same treatments were done at Kaikoura and Moeraki.

Durvillaea antarctica in New Zealand has a discrete reproductive period from Autumn (May/ June) to Spring (September/ October) . Consequently, I tested the effect of clearing canopy and coralline algae at different times. Identical treatments were initiated in Summer 1998/1999 (January 1999), Autumn 1999 (May 1999), Winter 1999 (August 1999), Spring 1999 (October1999) and Summer 1999/2000 (January 2000). Where possible treatments were randomised within sites but limited space meant that at some times treatments were randomly assigned within discrete areas. Plots were monitored prior to clearing and in May 1999, August 1999, October 1999, June 2000, March 2001 and October 2001.

Treatments were monitored using a 30 x 30 cm quadrat divided into 100 equally sized squares. Each treatment was visually assessed for the percentage cover of foliose algae, *Durvillaea*, encrusting coralline algae, turfing coralline algae, and bare rock; and invertebrate herbivores and *Durvillaea* recruits were counted. At three times (29/10/1999, 7/3/2001; 18/10/2001) the total lengths of recruits (< 1000 mm in length) in each quadrat was measured using Vernier calipers.

Table 5.2. Summary design of the canopy and substratum (+/- coralline algae) experiment testing their effects on the recruitment of *Durvillaea antarctica.*

Factor	n	Names		Fixed / Random
Peninsula/Sites	2	Kaikoura	Moeraki	Random
Canopy	2	+ Canopy	- Canopy	Fixed
Substratum	2	+ Corallines	- Corallines	Fixed
Replicates	4			
Clearance Times	5	Summer 98/99 Winter 1999 Summer 99/ 00	Autumn 1999 Spring 1999	

Quadrat sampling

The cover and abundance of *Durvillaea antarctica* recruits (<500mm) at First Bay and Seal Reef was monitored in 10 random 50 x 50 cm quadrats along a single transect in each of three habitats as recruits became visible in October 2001. These habitats were under, on the edge and outside adult canopies. The number of recruits grazed by the Butterfish, *Odax pullus,* in each quadrat was recorded.

Recruit transplants

Recruit transplants were done using *Durvillaea antarctica* recruits (<250mm total length), that were scraped from the substratum at First Bay and taken to the Edward Percival Field Station. The base of their holdfasts were blotted dry and then glued (Selleys 'Super-glue' ™) to fibre cement plates. Approximately 10 plants were glued to each plate. Each plant was mapped and its total length recorded. Plates were then transplanted across wave exposures and into treatments. Plates were attached to the substratum using a single screw and washer that was screwed into a plastic rawl plug (Ramset 8mm).

Across exposures

Initially, *Durvillaea antarctica* recruits were transplanted across wave exposure gradients at two sites within three levels of wave exposure around Kaikoura peninsula. Later, recruits were also transplanted across different sites within three levels of wave exposure on Banks peninsula and Kaikoura Peninsula.

Caging experiments

For the under, edge and outside canopy experiment roof treatments were used to exclude herbivorous fish. Rooves were 50 x 50 cm by 10 cm high metal frames that were bolted to the substratum. Plastic garden mesh (Nilex®, green 5 x 5 cm hole size) was cable tied to the top of the frame. Three plates (c.30 plants) were placed into 3 replicate cages under, on the edge and outside the *Durvillaea* canopy at Seal Reef (General Introduction,

Fig. 1.5B). At the same time 3 plates were transplanted without cages under, on the edge and outside the *Durvillaea* canopy. Outside canopy cages and no-cage treatments were repeated at First Bay. This was fortunate as the cages outside the canopies at Seal reef were destroyed by a storm shortly after the experiment began. Seal reef treatments were monitored 45 days after the experiment began and First Bay treatments were monitored 10 and 80 days after the experiment began. After these times all treatments were destroyed by another storm.

Across coastlines

Recruits from Kaikoura were also transplanted under and outside three cages at the 12 mile beach site near Greymouth on the west coast.

In all recruit transplant studies survival was not tested because the cause of disappearance could not be determined.

5.2.3 Data analysis

An analysis of variance (ANOVA) was used to test for treatment effects on the number and percentage cover of *Durvillaea antarctica* recruits at the end of the experiment in October 2001. Recruit numbers across clearance times were also compared after each reproductive season. Clearances done in Summer 1998/99, Autumn 1999 and winter 1999 were exposed to four reproductive seasons. Clearances started in Spring 1998 and Summer 1999/2000 were exposed to three reproductive seasons. After each reproductive season the effect of times of clearances on the number of recruits were analysed separately using ANOVA. For the model used, the main factors were Platform (random), Canopy (+/-, fixed) and Substratum (+/- coralline algae, fixed). Percent cover data were square-root arcsine transformed. Data were tested for homogeneity of variances using Cochran's test prior to analysis. If significant, data were either arcsine transformed or log-transformed (log $(_{n+1})$) prior to analysis. F-tests were used to examine differences in mean lengths of recruits between treatments and between clearance times. A mixed model

ANOVA done on quadrat the sampling data where the main factors were Site (random) and Canopy (Fixed). Tukey's HSD tests were used for *post hoc* comparison of means. In the recruit transplant experiments F-tests were used to examine differences in mean lengths of recruits between treatments. A non-parametric Kruskal-Wallis test was done to compare mean lengths of recruits transplanted across exposures at Kaikoura.

5.3 Results

5.3.1 Canopy and substratum clearances

Recruitment of Durvillaea antarctica

Generally, recruitment was highly variable between peninsulas and treatments and seasons but the major result was that in nine out of ten cases *Durvillaea antarctica* successfully recruited under adult canopies. Recruitment was greatest at Moeraki in the +canopy treatments in which the substratum had been cleared of coralline algae (Fig 5.1A-J). This was particularly evident in Summer 98 and Autumn 99 +canopy - substratum clearances in October 1999 at Moeraki where recruit numbers averaged between 150 and 300 per 0.09m^2 (Fig 5.1 F,G). Exceptions to this pattern were seen in the Summer 98, Winter 99 and Summer 99 - canopy treatments at Kaikoura where between 5 and 40 recruits per 0.25m^2 recruited at various times (Fig. 5.1 A-E). In three out of the five initiation times (Summer, Winter and Autumn 99) recruitment was greatest at Moeraki and by the end of the experiment in October 2001 there were significant differences in the number of recruits at the peninsula level in the Autumn 99, Winter 99 and Spring 99 initiated treatments (Table 5.3A). The effect of substratum at this time was only significant in the Winter 99 treatments where -coralline treatments generally had greater recruitment. The effects of Canopy treatments varied and they had different magnitudes of effects at each peninsula in the Summer 98 treatments. This was due to greater numbers of recruits in the -canopy -coralline treatments at Kaikoura. Canopy and Substratum also had different magnitudes of effects at the different peninsulas in the Autumn 99 initiated

treatments because only the +canopy - coralline treatment at Moeraki had significant numbers of *Durvillaea antarctica* recruits by October 2001.

Table 5.3. Summary of ANOVA tests of (A) the number and (B) the percent cover of *Durvillaea antarctica* recruits at the end of the experiment in October 2001. Significance levels: * (0.05), **(0.01), ***(0.001). Data were (A) $\log_{(n+1)}$ square-root, (B) square-root arcsin transformed ; all Cochran's tests were n.s.

Time of clearance:		Summer 1998/98		Autumn 1999		Winter 1999		Spring 1999		Summer 1999/2000	
Source	df	MS	F	MS	F	MS	F	MS	F	MS	F
A) Number of *Durvillaea* recruits											
Peninsula	1	0.31	0.27	7.72	7.06*	11.39	10.89**	13.43	8.21**	2.67	3.45
Canopy	1	1.69	0.22	1.36	27.49	4.77	2.23	0.56	0.10	0.02	0.01
Substratum	1	0.02	0.07	22.24	11.89	9.47	6062.00**	3.25	1.06	1.63	16.07
PxC	1	7.61	6.53*	0.05	0.05	2.13	2.04	5.41	3.31	1.68	2.17
PxS	1	0.35	0.30	1.87	1.71	0.01	0.01	3.07	1.88	0.10	0.13
CxS	1	0.08	0.16	3.24	0.41	2.01	37.39	0.01	0.01	3.83	14.75
PxCxS	1	0.53	0.45	7.93	7.25*	0.05	0.05	1.28	0.78	0.26	0.34
Error	24	1.16		1.09		1.05		1.64		0.77	
B) Percent cover of *Durvillaea* recruits											
Peninsula	1	0.28	0.16	0.07	0.36	6.77	3.51	0.39	0.17*	0.28	0.24
Canopy	1	4.44	0.21	4.47	1.45	13.18	1.91	0.31	0.02	1.98	0.36
Substratum	1	0.02	0.01	37.76	771.69*	11.86	1.02	0.17	0.12	2.95	3.68
PxC	1	20.90	12.03**	3.09	1.36	6.89	3.57	13.55	6.01	5.49	4.72*
PxS	1	7.00	4.03	0.05	0.02	11.62	6.02*	1.47	0.65	0.80	0.69
CxS	1	2.41	1.56	1.93	0.49	0.02	0.06	1.74	0.62	13.05	262.58*
PxCxS	1	1.55	0.89	3.97	1.75	0.36	0.18	2.80	1.25	0.05	0.04
Error	24	1.74		2.27		1.93		2.25		1.16	

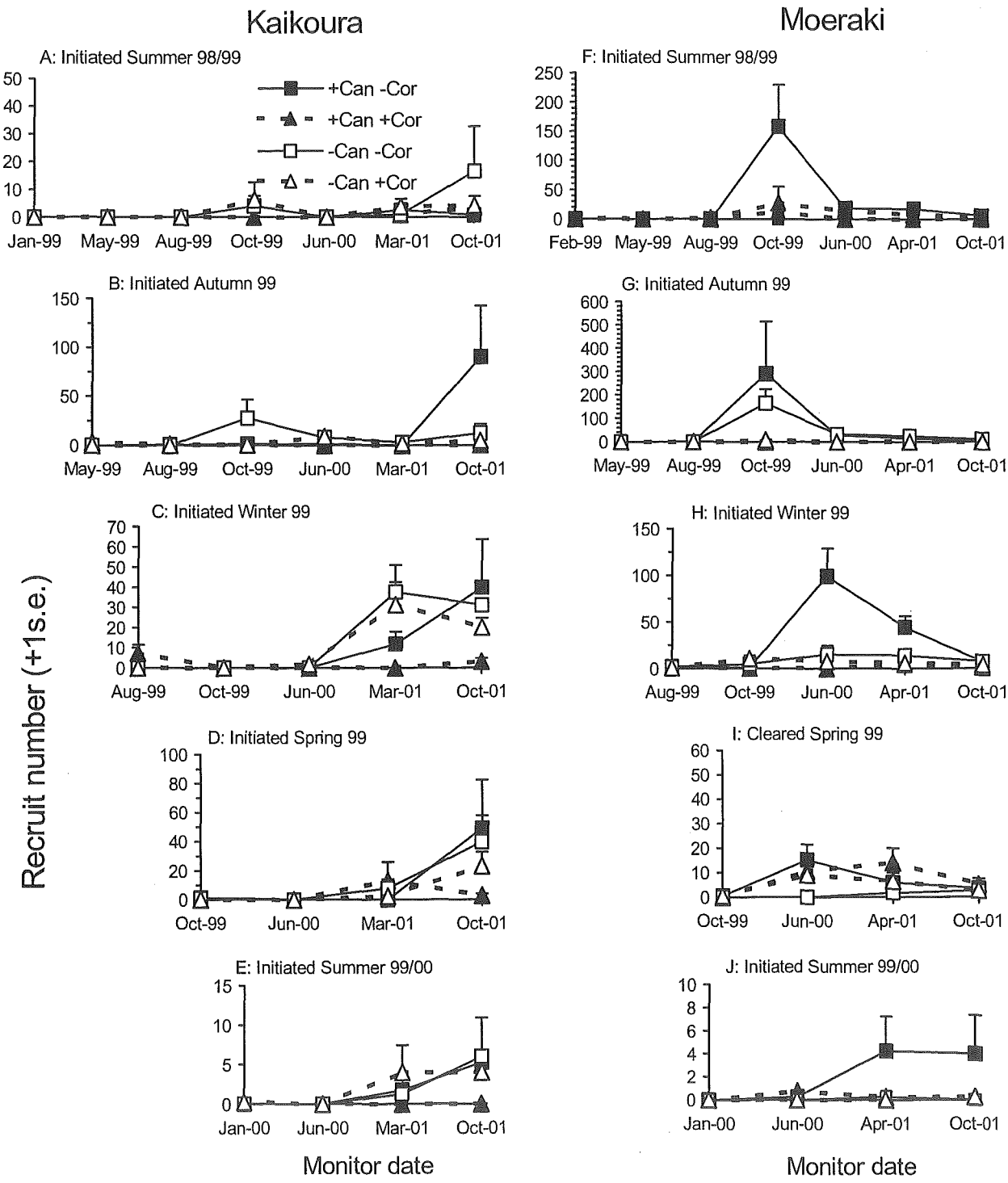

Figure 5.1. The average number of *Durvillaea antarctica* recruits (per 0.09m^2) through time for each treatment in the five initiation times in Summer 1998 (A, F), Autumn 1999 (B,G), Winter 1999 (C, H), Spring 1999 (D, I) and in Summer 1999 (E, J) at Moeraki and Kaikoura.

Percent cover of Durvillaea recruits

Percent cover of recruits was highly variable and showed few consistent patterns within or between treatments and peninsulas. This was generally greater in coralline removal treatments at Moeraki regardless of canopy presence or absence (Fig 5.2F-J). The cover of recruits at Kaikoura was more variable and was often initially greater in canopy removal treatments (Fig. 5.2A-D). However, in several cases recruit cover in -canopy treatments peaked and then declined or did not increase (Fig. 5.2B, D, E). This was because recruits were often grazed back to stipes by the butterfish *Odax pullus*. By the end of the experiment in October 2001 canopy treatments had different magnitudes of effects at different peninsulas in the Summer 98 initiated treatments due to greater recruit cover in +canopy treatments at Moeraki but greater cover in canopy removal treatment at Kaikoura (Table 5.3B; Fig. 5.2A,B). At the same time substratum significantly affected the percent cover of recruits in the Autumn 99 treatments because -coralline treatments had a greater cover of recruits at both peninsulas. The Winter 99 initiated canopy removal treatments at Kaikoura were the only treatments in any clearance time to reach one hundred percent cover. Recruit cover in the Spring 99 treatments at both peninsulas remained low but was different at each peninsula. Canopy treatments had different magnitudes of effects on recruit cover on the different substrata and at different peninsulas in the Summer 98 treatments by October 2001 (Table 5.3B), because there was a greater cover of recruits in the +canopy -coralline treatments at Moeraki but at Kaikoura the greatest cover was in the -canopy +coralline treatments (Fig. 5.2E,J).

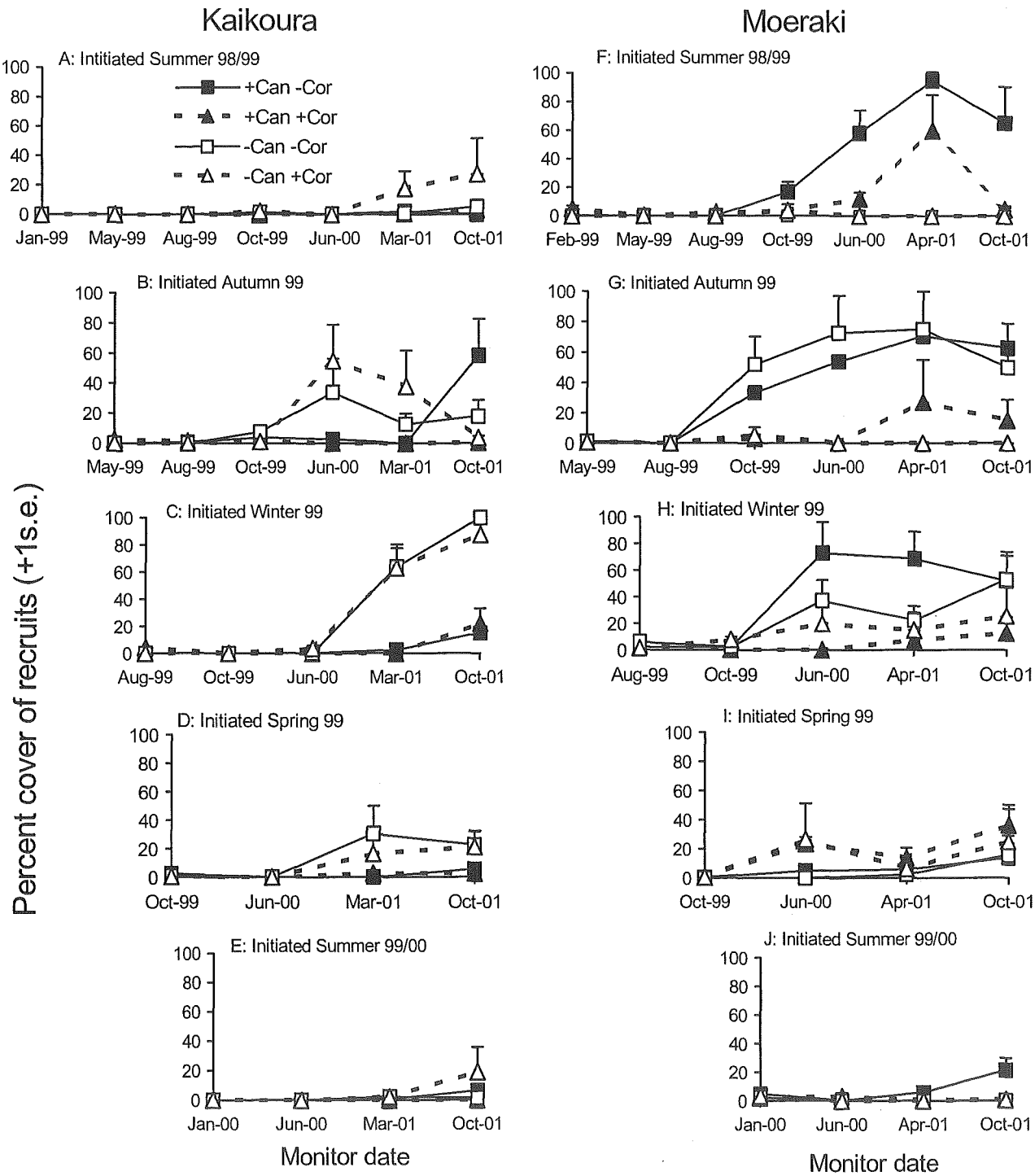

Figure 5.2. The average percent cover of *Durvillaea antarctica* recruits through time for each treatment in the five initiation times in Summer 1998 (A, F), Autumn 1999 (B,G), Winter 1999 (C, H), Spring 1999 (D, I) and in Summer 1999 (E, J) at Moeraki and Kaikoura.

Durvillaea lengths

In many cases decreases in average length were observed due to grazing by butterfish, with many plants grazed back to stipes (Fig 5.3). In several cases average plant lengths in canopy clearance treatments declined or did not increase by October 2001 after peak lengths in June 2001. This was particularly evident in the Summer 98/99 and Spring 99 -canopy +coralline treatments at Kaikoura (Fig. 5.4A,D), and in the Winter 99 canopy clearance treatments and the Spring 99 -canopy +coralline treatment at Moeraki (Fig. 5.4H,I).

At the end of the experiment in October 2001 *Durvillaea antarctica* recruits at Moeraki in Summer 98 and Autumn 99 initiated treatments (Fig. 5.4F,G), were significantly longer than plants in the same treatments at Kaikoura (Fig. 5.4A,B; Summer 98: $F_{(36,4)}=487.55$, $p<0.01$; Autumn 99: $F_{(62,46)}=107.63$, $p<0.001$;). The plants at Moeraki reached an average length of c.750mm (Fig. 5.4F,G) while the same treatments in Kaikoura reached an average length of c. 200-300mm by October 2001. Generally, recruit lengths varied between treatments, clearance times and sites by October 2001 (Fig. 5.4). For example, -canopy treatments had longer plants in the Autumn 99, Winter 99 and Spring 99 clearances at Kaikoura but the largest plants in both Summer initiated treatments were in the +canopy -coralline clearances (Fig. 5.4A-E). Similarly, at Moeraki the Summer 98, Spring 99, and Summer 99 initiated treatments +canopy treatments had the longest plants (Fig. 5.4F-J).

Figure 5.3. Picture of *Durvillaea antarctica* recruits grazed down to stipes in –canopy treatments at Kaikoura.

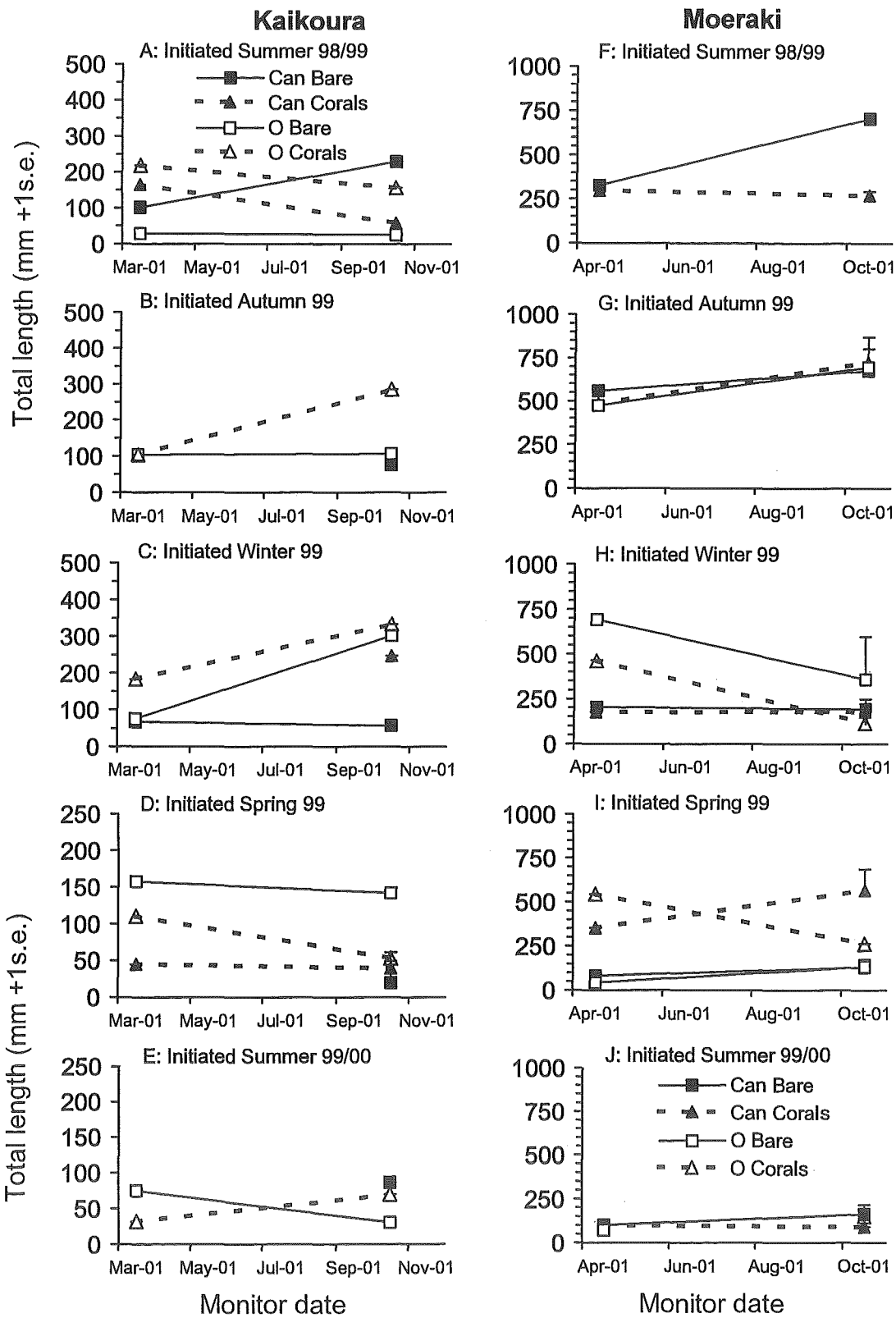

Figure 5.4. The average total lengths of *Durvillaea antarctica* recruits monitored in April 2001 and October 2001 in each treatment for the five initiation times Summer 1998 (A, F), Autumn 1999 (B,G), Winter 1999 (C, H), Spring 1999 (D, I) and in Summer 1999 (E, J) at Moeraki and Kaikoura.

Cover of other foliose algae

There was considerable variation in the cover of other species of algae across clearance times and treatments (Fig. 5.5). The cover of other algae, in most cases, increased quickly in coralline removal treatments regardless of canopy cover largely due to settlement of ephemeral algae and brown and green diatomaceous films. One exception was the Autumn 99 clearances at Kaikoura that remained largely devoid of other algae until October 1999 and June 2000 when other species recruited in to canopy clearance treatments (Fig. 5.5B). In general, other species of algae took longer to invade –canopy +coralline treatments. However, by October 2001 cover of other algal species generally increased in this treatment to levels much higher than at the start of the experiment. This trend occurred at all clearance times at Kaikoura where the most common species were *Halopteris virgata, Carpophyllum maschalocarpum, Gelidium ceramoides* and the ephemeral foliose stage of *Scytosiphon lomentaria*. The same trend was seen in all but the Winter 1999 clearance time at Moeraki where common algae included small plants of *Macrocystis pyrifera, Hormosira banksii, Cystophora torulosa* and *Halopteris virgata*. Other common species at Moeraki in -canopy +coralline treatments by October 2001 included *Pleonosporium hirtum, Ballia callitricha* and *Glossophora kunthii*. By October 2001 the only significant interaction effect was a that between Peninsula and Substratum in the Autumn 99 clearances (Table 5.4A). This was caused by lower recruitment of other algae into +canopy +coralline treatments at Moeraki (Fig. 5.5G). Canopy also significantly affected the percentage cover of other algae in the Summer 99/00 clearances in October 2001 because there was generally greater recruitment of other algae into -canopy treatments (Fig. 5.5E,J).

Table 5.4. Summary of ANOVA test of the percent cover in each time of clearance of A) other foliose algae and B) turfing coralline algae at the end of the experiment in October 2001. Significance levels: * (0.05), **(0.01), ***(0.001). Some data were ([a]) $\log_{(n+1)}$ transformed or ([b]) arcsin transformed all Cochran's tests were n.s.

Time of clearance:		Summer 1998/98		Autumn 1999		Winter 1999		Spring 1999		Summer 1999/2000	
Source	df	MS[a]	F	MS[a]	F	MS[a]	F	MS[a]	F	MS[a]	F
A) Other foliose algae											
Peninsula	1	0.24	0.21	0.23	0.18	0.59	0.40	3.62	2.41	60.50	0.28
Canopy	1	40.54	297.46	9.86	28.84	3.99	30.44	10.54	3.52	10011.13	556.17*
Substratum	1	3.67	10.19	0.79	0.06	0.01	0.01	0.51	0.36	1200.50	4.74
PxC	1	0.14	0.12	0.34	0.27	0.13	0.09	3.00	1.99	18.00	0.08
PxS	1	0.36	0.32	13.31	10.32**	1.38	0.94	1.43	0.95	253.13	1.18
CxS	1	0.27	3.60	2.13	0.45	0.46	3.32	0.15	0.15	200.00	0.24
PxCxS	1	0.07	0.07	4.77	3.70	0.14	0.09	0.95	0.63	820.13	3.81
Error	24	1.12		1.29		1.48		1.50		215.31	
B) Turfing coralline algae											
Peninsula	1	2.68	3.26	33.54	59.94***	18.93	79.88***	10.23	27.77***	6.43	20.05***
Canopy	1	1.42	632.09*	0.08	1.71	0.58	1.22	0.02	0.06	0.55	11.62
Substratum	1	0.86	27.00	0.01	0.05	0.11	0.96	1.82	1.86	0.50	1.86
PxC	1	0.01	0.01	0.05	0.81	0.47	2.00	0.26	0.71	0.05	0.15
PxS	1	0.03	0.04	0.06	0.11	0.12	0.50	0.98	2.65	0.27	0.83
CxS	1	0.81	4.37	1.47	0.66	0.81	4.45	0.01	0.71	0.01	0.03
PxCxS	1	0.19	0.23	2.23	3.98	0.18	0.77	0.01	0.03	0.22	0.70
Error	24	0.82		0.56		0.24		0.37		0.32	

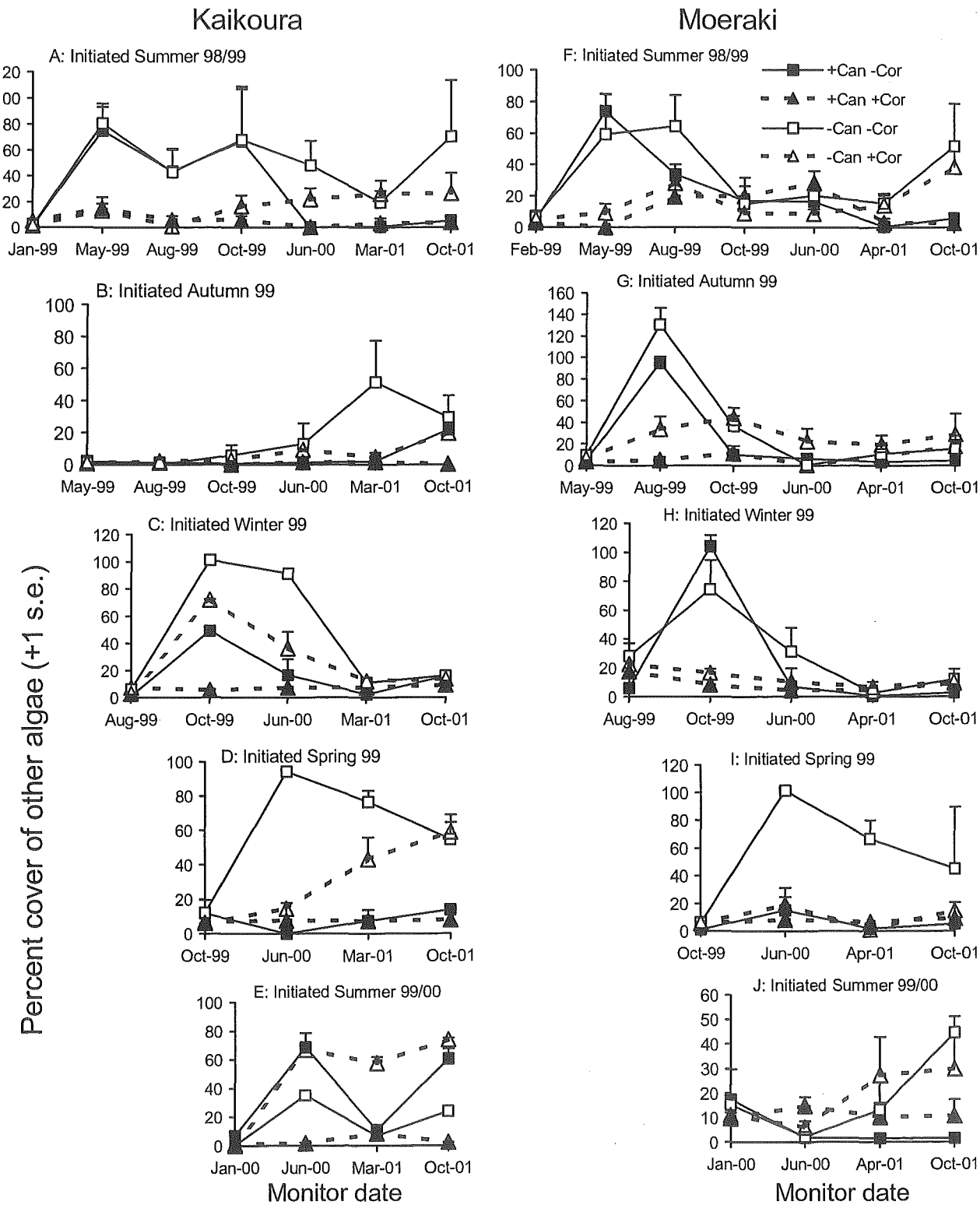

Figure 5.5. The mean percent cover of other foliose algae through time for each treatment in the five initiation times in Summer 1998 (A, F), Autumn 1999 (B,G), Winter 1999 (C, H), Spring 1999 (D, I) and in Summer 1999 (E, J) at Moeraki and Kaikoura.

Turfing coralline percent cover

The cover of turfing corallines in treatments fluctuated over the course of the study and depended on peninsulas and clearance time (Fig. 5.6). Generally, turfing corallines were more abundant at Moeraki prior to removal and in most cases increased in cover when *Durvillaea antarctica* canopies were cleared. However, the recovery to pre-clearance levels in coralline removal treatments took longer at Moeraki. One exception to this was the Summer 98/99 -canopy -coralline treatments at Moeraki that had double the original cover of turfing coralline algae by October 1999 (Fig. 5.6F). In contrast, the Winter 99 and Spring 99 coralline removal treatments at Moeraki had not reached pre-clearance cover by the end of the experiment in October 2001 (Fig. 5.6H, I). Removal of corallines and canopies at Kaikoura generally resulted in an increase in the cover of turfing coralline algae. This was particularly evident in the Summer 99/00 treatments in which turfing coralline cover increased from less than 20% to approximately 60% in the coralline removal and canopy clearance treatments (Fig. 5.6E). A similar pattern was observed in the Autumn 99 coralline algae removal treatments at Kaikoura (Fig. 5.6B). By the end of the experiment in October 2001 there were still significant differences in turfing coralline cover at the peninsula level in three out of the five clearance times (Table 5.4B), due mainly to the greater cover of coralline algae at Moeraki. Differences between the cover of coralline algae in the canopy treatments were only significant in the Summer 98 initiated treatments by October 2001.

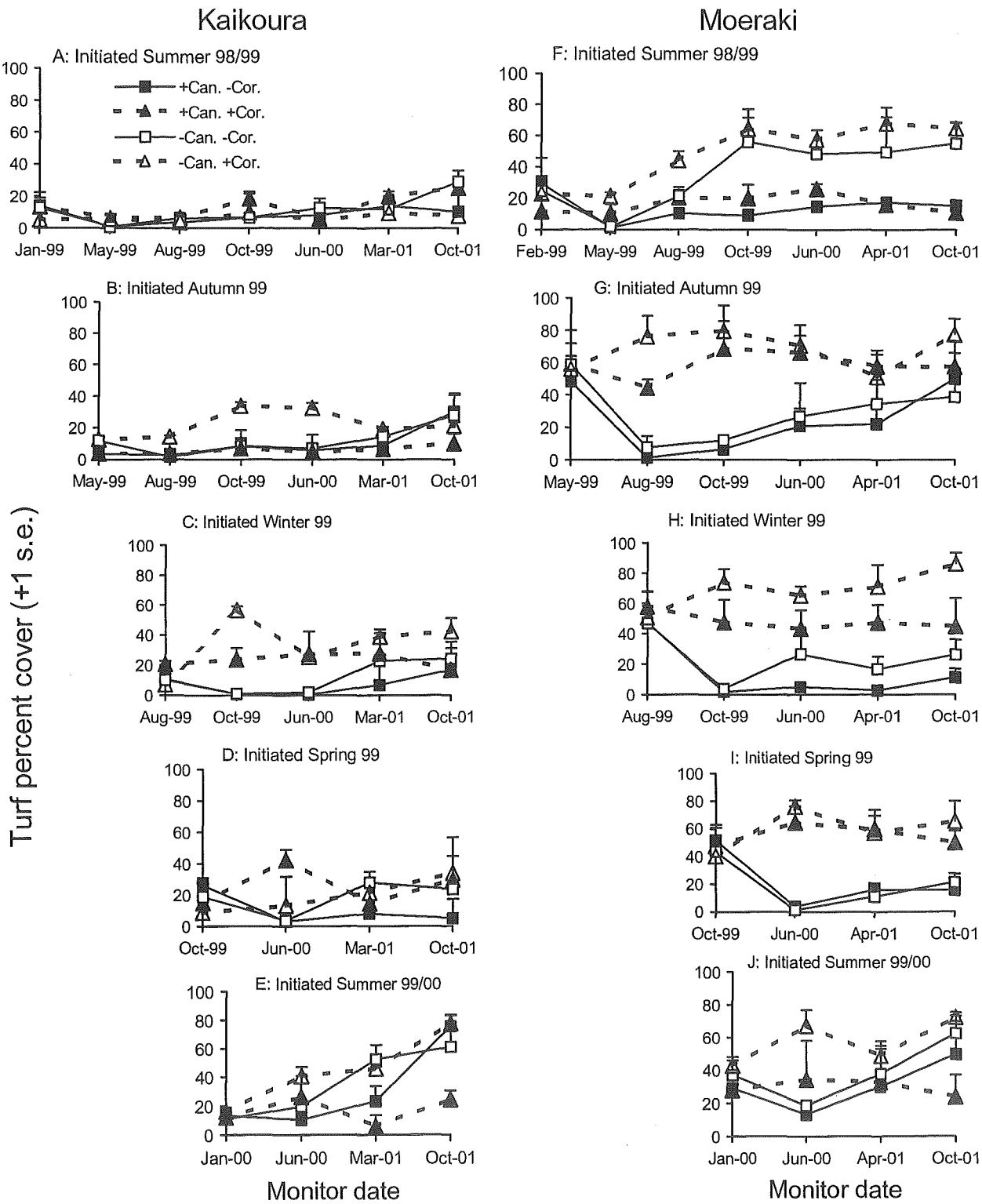

Figure 5.6. The mean percent cover of turfing coralline algae through time for each treatment in the five initiation times in Summer 1998 (A, F), Autumn 1999 (B,G), Winter 1999 (C, H), Spring 1999 (D, I) and in Summer 1999 (E, J) at Moeraki and Kaikoura.

5.3.2 Quadrat sampling

Quadrat samples of *Durvillaea antarctica* recruits under, on the edge and outside of *D. antarctica* canopies showed that recruits were most abundant outside canopies. For example at Seal reef on the Kaikoura peninsula recruit numbers averaged up to c.170 per $0.25m^2$ (Fig. 5.7). An ANOVA test showed there was no difference in the numbers of recruits between sites but a there was a significant site by canopy interaction ($F_{2,54}$ = 3.86, $p < 0.05$) because the effects of canopy on recruit numbers differed significantly between the two sites (Tukey HSD, $p < 0.01$). However, the percent of *D. antarctica* recruits with lunate bites from the butterfish *Odax pullus* was greater outside canopies (Tukey HSD, $p < 0.001$), particularly at First bay and this resulted in a lower percent cover of recruits (Fig 5.7). Many recruits had been grazed to stipes. At Seal reef despite a large percentage of plants with evidence of grazing a few recruits had escaped grazing resulting in a significantly greater percent cover outside canopies (Tukey HSD, $p < 0.01$; Fig. 5.7).

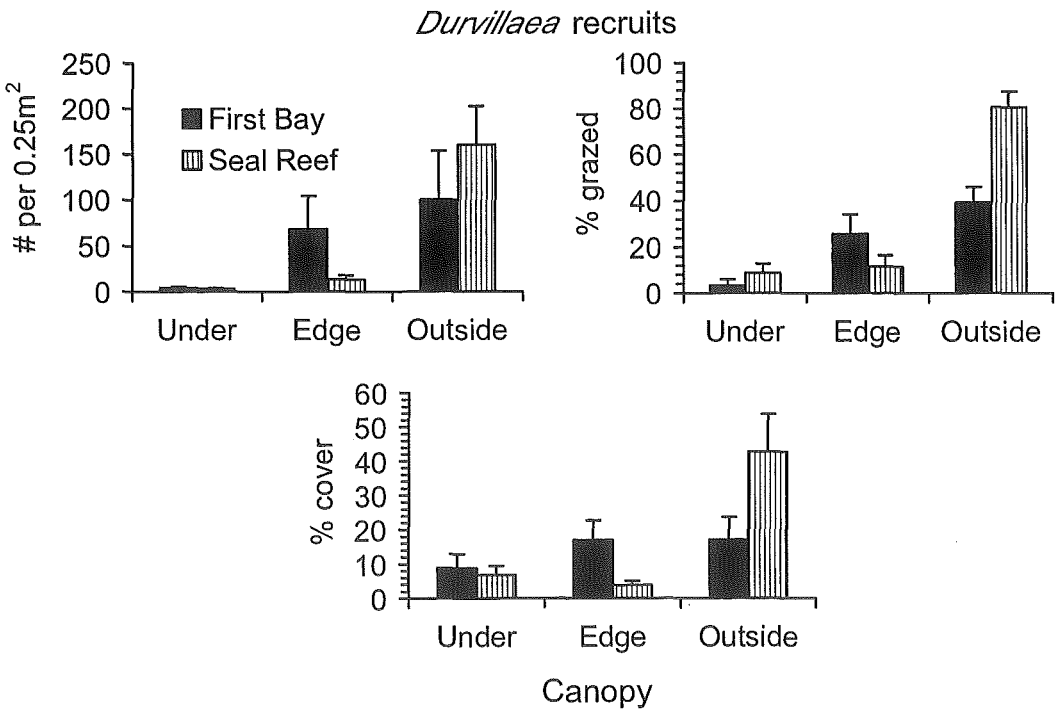

Figure 5.7. The overall number, the percent with evidence of butterfish grazing and percent cover of *Durvillaea antarctica* recruits under, on the edge and outside adult canopies at First Bay and Seal Reef sites at Kaikoura.

5.3.3 Recruit transplants

Durvillaea recruit transplants at Kaikoura

The first transplants of *Durvillaea antarctica* recruits were done between the exposed site at First Bay and the moderately exposed Carpark site on Kaikoura peninsula (Fig. 5.8). At the Carpark site of the five plants transplanted three were grazed down to their stipes within 100 days of transplanting. The two remaining plants survived a further 60 days before they were grazed down to the stipe by butterfish. During this period their growth was considerably slower than the five plants at First Bay and plants appeared physiologically stressed changing to a pale yellow colour. Shortly after this change was observed the two plants that had grown to 63 and 85 cm in length were grazed down to the stipe and then down to their holdfasts. The bite marks in the plants indicated they had been grazed by the butterfish *Odax pullus*. Only one of the plants transplanted to First Bay was grazed by butterfish after 160 days. The remaining plants had grown to c.90 cm in length by this time.

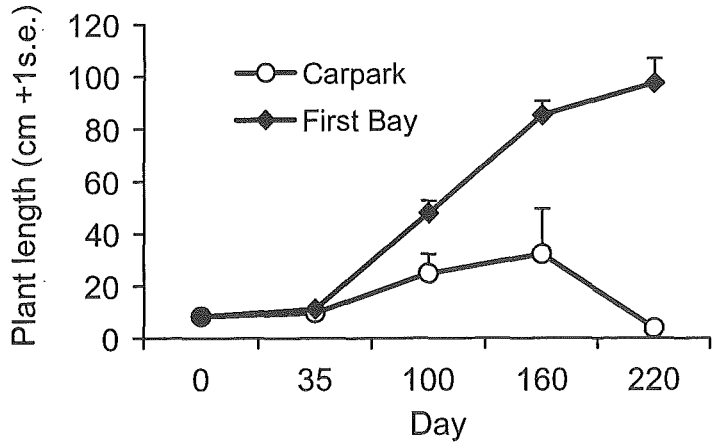

Figure 5.8. The average total length of *Durvillaea antarctica* recruits transplanted to First bay (exposed) and the Carpark site (intermediate exposure) at Kaikoura over time.

Across a wave exposure gradient

Durvillaea antarctica recruits transplanted to six sites around Kaikoura peninsula within three levels of wave exposure were grazed to stipes and in many cases down to holdfasts at all but the exposed sites within 60 days (Fig. 5.9). At this time there was a significant difference in the size of recruits across exposures (Kruskal-Wallis ANOVA, $H_{(2,\ n=61)} = 46.55$, $p<0.001$). Some growth was recorded at the second exposed site but at all other sites recruits were grazed by the butterfish *Odax pullus* (identified when caught in nets near transplants). No evidence of grazing was observed on other species of habitat-forming algae at sheltered and intermediate sites.

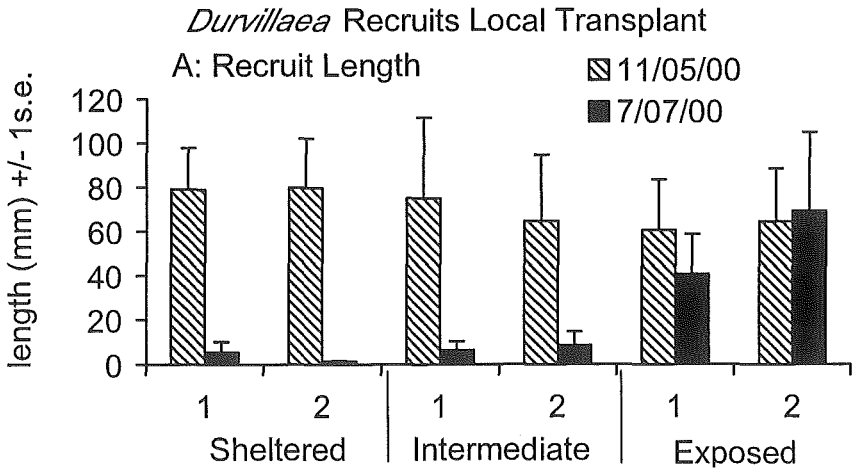

Figure 5.9. The average total length of *Durvillaea antarctica* recruits transplanted to sites across wave exposure gradients at Kaikoura at the beginning and end of the experiment two months later.

Transplants of Durvillaea recruit across peninsulas

Recruits transplanted across exposures on Kaikoura and Banks peninsulas were grazed back to their stipes at sheltered and intermediate sites (Fig. 5.10). Once again, lunate bites indicated the butterfish *Odax pullus* was responsible for grazing of recruits. At the exposed sites at Kaikoura transplanted recruits averaged c.300 mm in length after 217 days. At the exposed Banks Peninsula sites recruits averaged c.350 mm after the same time.

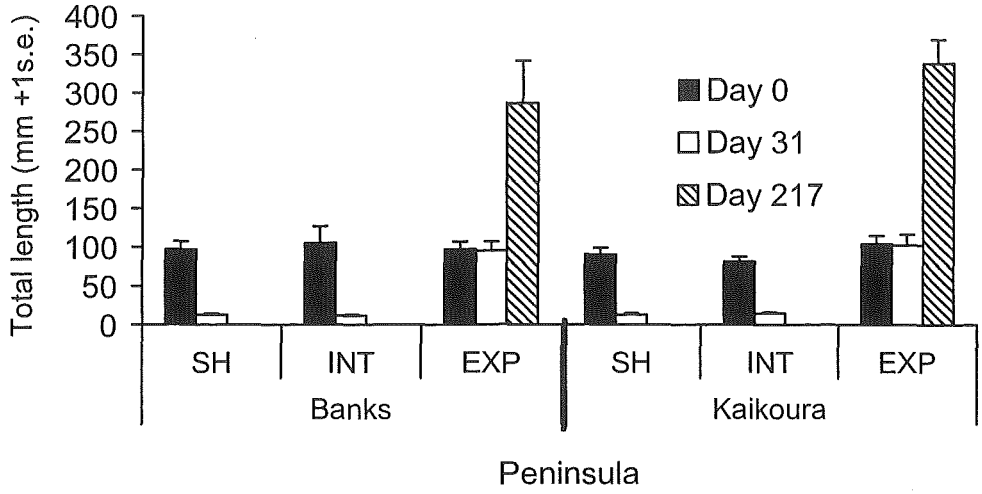

Figure 5.10. The average total length of *Durvillaea antarctica* recruits transplanted to sites across a wave exposure gradient on Banks and Kaikoura peninsulas at day 0, 31 and 217.

5.3.4 Caging experiments with Durvillaea recruits

Kaikoura

A caging experiment was done to exclude butterfish from transplanted recruits under, on the edge and outside *Durvillaea antarctica* canopies (Fig. 5.11A). However, the - canopy cages were lost at Seal reef in a storm. Fortunately, - canopy cages were also done at the same time at First bay and these were monitored at day 10 and day 80 (Fig. 5.11B). In all other treatments recruits grew c 20mm after 45 days and at this time uncaged recruits under the canopy were significantly longer than those on the edge ($F_{(2,4)} = 43.11$, $p < 0.01$) and outside ($F_{(2,3)}=0.02$, $p<0.01$) adult *D. antarctica* canopies. However, this was because almost all plants transplanted on the edge and outside adult canopies without cages were grazed to stipes. This was seen after 45 days at Seal reef and after 10 days at First bay. Some grazing occurred on open plants on the edge of the canopy. After 80 days *Durvillaea* recruits under cages at First bay had grown c. 190mm while those outside cages had been grazed down to holdfasts.

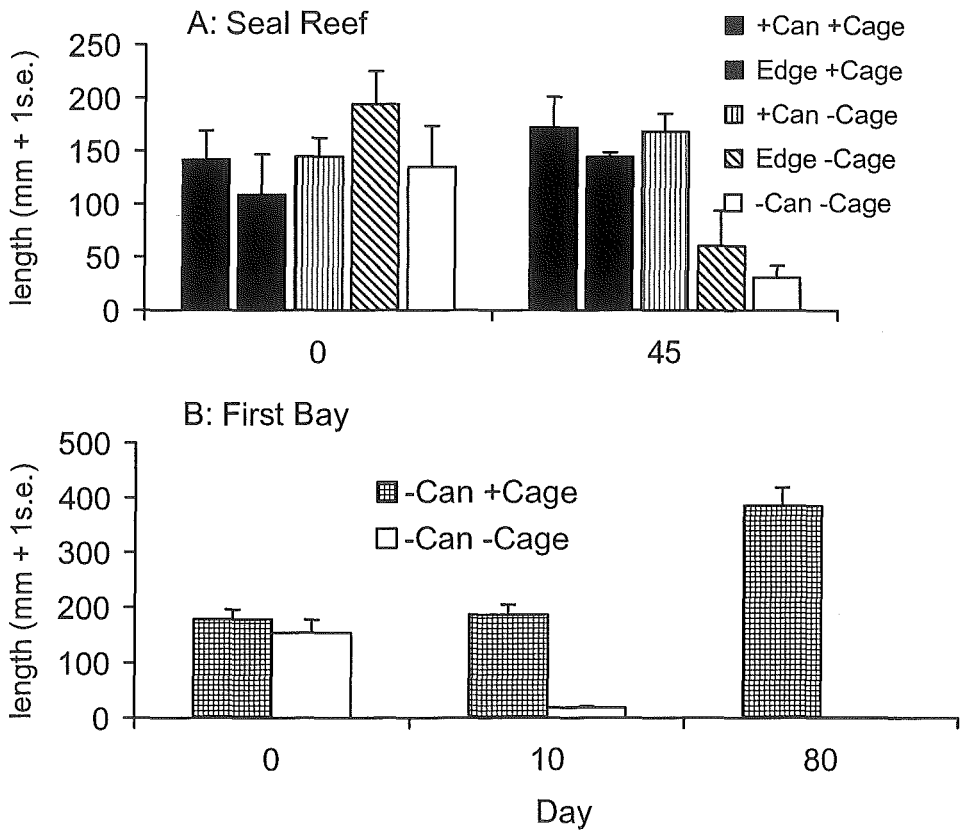

Figure 5.11. The average total length of *Durvillaea antarctica* recruits transplanted under, on the edge and outside adult canopies in +/- cage treatments at Seal Reef and +/- cages outside canopies at First Bay over time on Kaikoura peninsula.

5.4.5 Transplants to the West Coast

Recruits transplanted to the west coast were also grazed by butterfish when transplanted and did not grow outside cages within the first 40 days (Fig. 5.12). Plants in cages on the west coast grew c.40 mm within the first 40 days. Three larger plants transplanted outside cages were not grazed and had grown 100 mm after 150 days suggesting a size refuge from butterfish grazing may have been reached (Fig. 5.12).

Consequently, at day 150 there was no difference in the total length of recruits on caged and uncaged plates ($F_{(3,7)} = 0.39$, $p > 0.05$).

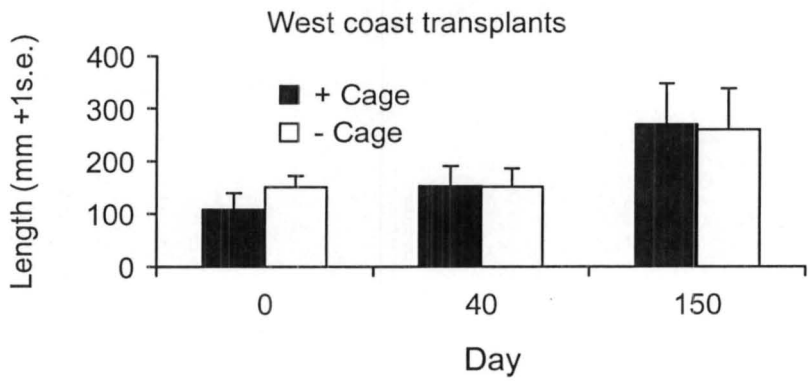

Figure 5.12. The total length of *Durvillaea antarctica* recruits transplanted from Kaikoura into +/- cage treatments away from adult canopies at 12-Mile Beach, Greymouth on the west coast of New Zealand.

Figure 5.13. Picture of *Durvillaea antarctica* recruits transplanted into +/- cage treatments at First Bay Kaikoura after 10 days. A caged treatment is on the right and uncaged is on the left.

5.4 Discussion

The experiments in this chapter were designed to test hypotheses relating to the recruitment of *Durvillaea antarctica* at two spatial scales. On a fine spatial scale I tested the importance of time of clearance, canopy and substratum on the recruitment and growth of *Durvillaea antarctica*. My results indicate that recruitment can occur directly under adult canopies, particularly when encrusting coralline algae are removed and that the presence of adult canopies of *D. antarctica* may facilitate recruitment in some cases by reducing fish grazing. The effects of substratum were complex but recruitment was generally lower in +coralline treatments but this effect varied with site. Furthermore, because of its relatively discrete reproductive period, the time of clearance affected the time taken for *Durvillaea antarctica* to successfully re-capture space.

On a larger spatial scale I used transplant experiments to test the effects of wave exposure and herbivory on the growth of *Durvillaea antarctica* recruits at sites on the east and west coast of the south island. Growth of recruits was expected to be greatest outside the adult canopies of *D. antarctica*. However, across exposures and coastlines recruits that were not protected from fish grazing were grazed down to stipes.

5.4.2. Canopy effects

In subtidal studies factors like shading, and possibly nutrient depletion, have been shown to inhibit intra and inter-specific recruitment under adult canopies (Dayton et al. 1984; Reed and Foster, 1984; Kennelly, 1987; Schiel, 1988). However, effects of adult canopies on recruitment of algae can depend on species. For example, Schiel (1980) found that the subtidal fucoid *Landsburgia quercifolia* was able to recruit under adult canopies of *Ecklonia radiata* in northeast New Zealand. My results indicate recruitment of *Durvillaea antarctica* can occur directly under adult canopies, particularly when coralline algae have been removed. Interestingly, Paine (1971) also observed of *Durvillaea antarctica* populations on the west coast of the North island "that it is capable of recruiting under its own shade".

That recruitment can occur directly under adult canopies is in contrast to many studies of subtidal populations of brown algae but is not similar to tat of intertidal brown algae (Brawley and Johnson, 1991). The ability of *Durvillaea antarctica* to recruit under adult canopies may be related to the turbulent nature of the wave exposed intertidal environment. The constant movement of adult canopies by waves may negate the impact of nutrient depletion and shading that affect recruitment in less turbulent subtidal environments (Reed and Foster, 1984; Kennelly, 1987; Schiel, 1990). Adult canopies of *Durvillaea antarctica* also appeared to protect recruits from fish grazing. This may have resulted from the 'whiplash' effects of adult fronds preventing fish from grazing recruits on the edge and under adult canopies. Other studies have found algal canopies to reduce grazing effects of invertebrate grazers. For example, Santelices and Ojeda (1990) suggest the effects of urchin grazing was reduced by adult canopies of the large brown alga *Lessonia nigrescens* allowing recruits to persist in gaps between adult holdfasts in central Chile. However, I found no examples in the literature of intertidal algae reducing fish grazing.

5.4.3. Timing of canopy removal

The time of canopy removal was important at both peninsulas with greatest recruitment of *Durvillaea antarctica* into autumn and winter clearances. For example, Summer 1998/1999 clearances at both peninsulas had minimal recruitment almost three years after the canopy was cleared because other species of foliose algae often captured space. Also, Spring 1999 and Summer 1999/2000 treatments had low recruitment at both peninsulas and two years after initiation. These results contrast studies of *D. antarctica* populations in central Chile where recruitment was observed year-round (Santelices et al., 1980; Santelices, 1990). However, my results are similar to those found in subtidal studies by Schiel (1988) who showed that, in northern New Zealand, seasonal recruitment of subtidal populations of algae was a major factor in determining which species captured space after disturbance.

5.4.4. Effects of Coralline algae

In general, recruitment of *Durvillaea antarctica* was initially greater in treatments where all coralline algae had been removed, regardless of canopy presence but later the development of turfing coralline assemblages appeared to facilitate recruitment. The relationship between recruitment of large perennial algae and coralline algae can be complex and variable. Encrusting coralline algae appear to inhibit recruitment of other algae through sloughing of epithallial cells (Johnson and Mann, 1986; Vadas et al. 1992; Camus, 1994). For example, Camus (1994) suggested that, through the shedding of epithallial cells, encrusting corallines reduced the recruitment of *Lessonia nigrescens* in central Chile. In another example, Worm and Chapman (1996) found the recruitment of *Fucus evanescens* was inhibited by the crustose alga *Chondrus crispus* that prevented successful attachment of young plants. In my study, encrusting coralline algae dominated the subcanopy prior to removal of *D. antarctica* canopies which may inhibit recruitment. However, turfing coralline algae that developed once *D. antarctica* canopies were removed increased recruitment.

In contrast, turfing coralline algae, have been shown to facilitate the recruitment of several species of fucoid algae (Brawley and Johnson, 1991; Benedetti-Cecchi and Cinelli, 1992; Brawley and Johnson, 1993). For example, using agarose beads, Brawley and Johnson (1991) found that the microhabitat provided by turfing corallines provided protection from desiccation for zygotes of *Pelvetia fastigiata*. Benedetti-Cecchi and Cinelli (1992) showed recruitment of *Cystoseira* in rock pools on the west coast of Italy was enhanced 2-3 fold by the presence of algal turfs.

At both Moeraki and Kaikoura, turfing coralline cover increased once *Durvillaea antarctica* canopies were removed; probably due to a reduction in 'whiplash' effects. Turfing coralline algae are often among the first species to colonise disturbed areas in lower intertidal zones (Hay, 1981; Menge et al., 1993). Other studies, have shown macroalgal canopies can maintain and facilitate encrusting coralline habitat while

inhibiting turfing coralline algae. For example, in a recent study in south Australia, Melville and Connell (2001) found using reciprocal transplants of turf and encrusting coralline boulders, that subtidal *Ecklonia radiata* canopies, rather than simply co-occurring with encrusting coralline algae, actually facilitated its growth and survival by inhibiting turfing coralline algae. In my study, the recovery of turfing coralline algae appeared to facilitate the recruitment of *Durvillaea* into the Winter 99 and Spring 99 -canopy +coralline algae treatments at Kaikoura almost three years after clearing, and the increased the recruitment of other species of algae into the same treatment at all clearance times.

Facilitation of *Durvillaea antarctica* recruitment into my treatments may have resulted from a reduction in invertebrate grazing effects, a result found in other intertidal studies. For example, in the low intertidal zone in central Chile, Camus (1994) found turfing coralline algae facilitated recruitment of the large brown alga *Lessonia nigrescens* by reducing grazer effectiveness. However, Kenelly (1987) found the opposite applied for the kelp *Ecklonia radiata* in southern Australia, where turfing corallines inhibited recruitment through some process other than its physical presence because plants also failed to recruit into turfing coralline removal areas.

5.4.5. Recruitment of other algae

The recruitment of other algae into canopy clearance areas was closely related to the proximity of other algal habitats but did not appear to affect *Durvillaea antarctica* recruitment. At Moeraki, large beds of *Cystophora torulosa*, *Hormosira banksii* and *Xiphophora chondrophylla* on the periphery of the *D. antarctica* habitat resulted in the recruitment of small plants of these species into turf covered canopy clearance treatments by the end of the study. At Kaikoura other species like *Carpophyllum maschalocarpum* and *Halopteris virgata* were more abundant on the edge of *D. antarctica* canopies and invaded the same treatments.

Recruitment of algae into disturbed intertidal areas is largely determined by clearance time, size of clearance, grazing and the reproductive and dispersal characteristics of the algal species (Paine 1984; Sousa, 1984; Schiel; 1988; Farrell, 1989; Menge et al., 1993; Kim and De Wreede, 1996; McCook and Chapman, 1997). For example, Sousa (1984) found that grazers were more abundant and had a greater impact on algal recruitment in smaller clearances in mussel beds in central California but that dispersal abilities had a significant impact on recruitment into larger clearances. Kim and De Wreede (1996) found that medium sized gaps in high shore algal habitats in British Columbia were recolonised faster than small and large gaps. They suggest slower recovery of smaller gaps was due to shading and whiplash effects that the slow recovery of larger gaps may have been due to desiccation stress and dispersal limitations of component species.

Dispersal limitation in algae is related to the hydrodynamic environment (Gaylord et al., 2002), the life history characteristics (Clayton, 1990) and behaviour of spores (Reed et al., 1988, Amsler et al., 1992). In my study dispersal limitation was unlikely to have affected *Durvillaea antarctica* recruitment. However, it may have affected the recruitment of other species of fucoid algae that are often poor dispersal potential (Chapman, 1995; Reed et al., 2000; Gaylord et al, 2002). The 30 x30 cm size of coralline removals in my study is similar to those found naturally when adult holdfasts detach (Pers. Obs.), and as discussed in Chapter 3, the relatively buoyant spores released in copious quantities of buoyant mucilage probably give *D. antarctica* greater dispersal capabilities than other common intertidal fucoids in New Zealand like *Cystophora torulosa* and *Hormosira banksii*. Even large gaps in *D. antarctica* canopies are, therefore, likely to be swamped with *D. antarctica* zygotes during the reproductive season.

Ephemeral algae and diatomaceous films were the first species to colonize coralline removal treatments and their cover decreased as *Durvillaea antarctica* cover increased. In my study no immediate effects of ephemeral algae on the recruitment of *D. antarctica* were found. This result is in contrast to several studies of algal succession higher in the intertidal zone where recruitment of fucoid algae is often suppressed by ephemeral

algae slowing succession (Lubchenco, 1978; Hawkins and Hartnoll, 1983; Cubit, 1984; Kim, 1997). For example, Kim (1997) found recruitment of *Fucus gardneri*, in the upper intertidal zone in British Columbia, was slowed when limpet grazers were excluded and a cover of ephemeral algae dominated. However, Hay (1979b) documented similar results in a limpet removal experiment in Kaikoura. He found *D. antarctica* quickly recruited into areas dominated by ephemeral algae if limpets were removed during *D. antarcticas* reproductive season; even though limpet removals were above the usual distribution of *D. antarctica*. Ephemeral algae does not appear to inhibit recruitment of this habitat-forming algae.

5.4.6. Fish grazing effects

I transplanted recruits stages of *Durvillaea antarctica* in an attempt to explain its absence from more sheltered areas that were, in some cases, less than 100 metres from adult canopies. I also transplanted recruits to sites on the West coast of the south island to explain its low abundance on this highly productive coastline (Menge et al. 1999). Despite repeated transplants, *Durvillaea antarctica* recruits placed away from adult canopies were grazed down to the stipe by the butterfish *Odax pullus*. This resulted, in most cases, in the eventual death of the recruits.

This is significant because, while there are several examples of invertebrate grazers controlling algal abundance in the lower intertidal and subtidal zones (Sousa et al., 1981; Andrew and Underwood, 1989; Jones and Andrew, 1990; Andrew, 1993), no examples of herbivorous fish controlling the distribution and abundance of intertidal large brown algae could be found in the literature. There are examples from subtidal studies. For example, in the Mediterranean sublittoral, Sala and Boudouresque (1997) found experimental reduction of fish grazing lead to dramatic changes in algal community structure with significant increases in the abundance of fleshy erect algae. Also, Andrew and Jones (1990) describe the formation of patches by *Odax cyanomelas* in *Ecklonia radiata* forests in NSW. They found that during spring adult female *O. cyanomelas* cleared patches

of adult *Ecklonia* near territorial males creating single age cohorts in patches. This contrasts the effects of grazing by *Odax pullus* on *D. antarctica* in my study, that occurred year round and mainly on recruit stages.

In general, examples of fishes controlling the distribution and abundance of intertidal algae are not common in the literature. However, recent feeding and dietary studies suggest their importance may have been underestimated. For example, Horn et al. (1982) show that a large percentage of the energy obtained by the intertidal fishes *Cebidichthys violaceus* and *Xiphister mucosus* near Piedras Blancas, California, is derived from a diet of mainly intertidal red and green algae. They found seasonal changes in the fishes diets with both fish preferring *Iridaea flaccida* (now *Marziella flaccida*) during winter and annual red algae like *Porphyra perforata* and *Microcladia coulteri* during summer. More recently, Ojeda and Munoz (1999) provided an experimental example of fish grazing determining algal abundance in a temperate intertidal environment on the coast of central Chile. Their results show that, grazing by the herbivorous fish *Scartichthys viridis* had significant effects on the algal community structure in the mid intertidal zone by reducing the cover of the green alga *Ulva rigida* and the red alga *Gelidium chilense*. No examples of fish controlling intertidal brown algae abundance were found.

5.4.7. Fish herbivory

Fish herbivory has important ecological implications for shallow subtidal and intertidal assemblages by facilitating nutrient transfer from primary producers to the wider community, and through effects on the distribution and abundance of primary producers and habitat-forming algae (Meekan and Choat, 1997). Fish herbivory has also been implicated in the evolution of chemical and structural defences in several species of marine algae through selective grazing (Horn, 1981; Hay et al., 1988a, b, 1990, 1994; Hay, 1991a, b, 1996) but the relative importance of chemical defences is an area of some debate (Hay, 1996; Choat and Clements, 1998).

Because of logistical constraints and researcher preferences much of the work on fish herbivory has been done in the clear waters around tropical coral reefs where herbivorous fishes can have significant effects on algal biomass and distribution (Sammarco, 1983; Lewis and Wainwright, 1985; Carpenter, 1986; Lewis, 1986), and are up to 25 percent more abundant than in temperate habitats (Meekan and Choat, 1997). Consequently, several studies have concluded that the role herbivorous fish play in algal community dynamics in temperate environments is probably relatively small and localised (Choat and Schiel, 1982; Hawkins and Hartnoll, 1983; Jones and Andrew, 1990). However, my results suggest fish herbivory, particularly by the butterfish *Odax pullus*, plays a major role in determining the distribution and abundance of the large brown habitat-forming alga *Durvillaea antarctica*.

The butterfish, *Odax pullus*, of the family Odacidae, is common in shallow subtidal regions as far south as 44° around New Zealand (Choat and Ayling, 1987; Schiel, unpublished data). The majority of studies on this fish have been done on populations in North eastern New Zealand (Clements, 1985; Choat and Clements, 1992; Choat and Clements, 1993; Clements and Choat, 1993; Clements et al., 1994; Meekan and Choat, 1997), where its nutritional ecology, diet and feeding rates have been examined and compared to other herbivorous fish species in New Zealand and Australia. The diet of *Odax pullus* changes with life-stage. For example, Clements and Choat (1993) found juvenile *O. pullus* in North eastern New Zealand consumed a greater percentage of gastropods and red algae than adults. *O. pullus* adults fed selectively on Laminarian algae and the reproductive thalli of fucoids algae despite high concentrations of secondary metabolites. Choat and Clements (1993) suggest that changes in diet are related to changes in gut length, feeding anatomy that affected bite strength, and nutritional requirements related to growth. *Odax pullus* lacks a true stomach and relies on endosymbionts in its elongated posterior intestine to process short-chain fatty acids from ingested brown algae (Clements et al., 1994).

The explicitly herbivorous *O. pullus* is fairly unique and contrasts other Odacid and Aplodactylid fish from Australia and New Zealand. Choat and Clements (1993) showed that *Odax acroptilus* on the central coast of NSW consumed mainly detritus with a mixture of animal material and some algal thalli, while other herbivorous fishes from northern New Zealand *Aplodactylis arctidens* and *Girella tricuspidata* fed mainly on red foliose and filamentous algae. In their recent review paper, Choat and Clements (1998) propose that the temperate herbivorous fishes of the Odacidae and Kyphosidae families are the only explicitly herbivorous fish because the majority of tropical herbivorous fish consume mixtures of detritus and animal material along with algae. They suggest that a nutritional ecology approach is necessary to understand the role of secondary metabolites in determining diets of herbivorous fish.

Even within species there appear to be distinct changes in diet with latitude. Russel (1983) found the gut contents of *Odax pullus* at all of his northern sites consisted almost exclusively of reproductive parts of *Carpophyllum maschalocarpum.* In studies of more southern *O. pullus* populations around Wellington, Clements (1985) and Meekan (1986) found *Lessonia variegata* was the principle component of gut contents. More recently, Bader (1998) described the distribution and abundance, feeding and behaviour of *Odax pullus* around Kaikoura peninsula. Bader (1998) also found the diet of *O. pullus* was different to those described for populations north eastern New Zealand and that a major percentage (>50%) of their diet for most of the year consisted of *Lessonia variegata,* a flat bladed brown alga common around Kaikoura peninsula that is similar in thickness and colour to *Durvillaea* recruits.

5.4.8. Physiological tolerances of Durvillaea

Prior to grazing, *Durvillaea antarctica* plants at sheltered and intermediate sites often became discoloured and generally appeared stressed despite being placed in the lower tidal zone (Per. Obs.). A possible explanation for this phenomenon may relate to the calmer conditions preventing the transfer of nutrients across the boundary layer that surrounds blades (Hurd and Dring, 1990, 1991; Hurd, 2000). This could have lead to

increased physiological stress and may have increased palatability by reducing plant toughness. Choat and Clements (1993) suggest bite strength may determine the ability of *Odax pullus* to graze on certain algae. Alternatively, physiological stress may have reduced concentrations of secondary metabolites that may deter fish grazers when found in greater concentrations (Hay, 1991, 1996). Consequently, stressed *D. antarctica* recruits may have been selectively grazed as they became softer and easier to consume relative to the harder fucoid algae, like *Hormosira banksii* and *Cystophora torulosa,* that dominate in more sheltered areas. No evidence of butterfish grazing was observed on either of these species.

5.4.9. West Coast abundance

Physiological stress does not, however, explain the low abundance of *Durvillaea antarctica* at exposed west coast sites (see Chapter 2). Menge et al. (1999) suggest that the same west coast sites experience more frequent up-welling of oceanic waters than several east coast sites and should, therefore, be more productive. Using transplants of *Durvillaea antarctica* recruits into the lower tidal zone at the same west coast site I found that grazing by the butterfish *Odax pullus* was largely responsible for its low abundance. Examples of natural populations being completely grazed to stipes were also observed (Pers. Obs.). However, several larger plants transplanted outside cages on both the east and west coast did appear to reach a size refuge from grazing.

5.4.11. Summary

Despite extensive searches no examples of herbivorous fish controlling the abundance and distribution of intertidal brown algae could be found. The unique results found in this study suggest the butterfish *Odax pullus* will selectively feed on *Durvillaea antarctica* recruits that settle outside adult canopies in the south island of New Zealand. This has several important ecological implications. First, by restricting the spread of *Durvillaea antarctica* into more sheltered situations it allows other species of algae, that would be negatively effected by *D. antarctica* canopy effects, to recruit and dominate. Second, because *D. antarctica* is a major source of biomass and primary production,

grazing by butterfish no doubt has a significant effect on the nutrient cycling within these intertidal communities. Third, the lack of grazing on other species of algae in more sheltered conditions suggests there may be a toughness refuge from butterfish grazing (Clements and Choat, 1993) or that some algae are less palatable or nutrient poor (Choat and Clements, 1993, 1998) or they have chemical defences that deter butterfish grazing (Hay, 1991,1996). Understanding the relative importance of these factors will help determine the role of fish herbivory in affecting the distribution and abundance of habitat-forming algae.

Chapter 6

GENERAL DISCUSSION

6.1 General discussion

A key component in my study was the use of multi-factorial designs, a standard substratum and early life stages of habitat-forming algae across wave exposure gradients at local, regional and hemispheric scales. The central objective of my thesis was to test predictions of community structure models pertaining to interactions between herbivores and plants across gradients in wave exposures. My findings contrast several predictions of 'Environmental Stress Model' proposed by Menge and Sutherland (1987) relating to the relative importance of grazing across gradients of environmental stress. I found grazers removed germlings of habitat-forming algae regardless of wave exposure in New Zealand and Oregon. This is significant because few studies have successfully tested the predictions of community structure models, such as the 'Environmental Stress Model' (Menge and Sutherland, 1987), because of the complex nature of the biological and environmental variables they encompass and the difficulties in controlling for confounding variables (see general introduction). Another difficulty in testing predictions of environmental stress models arises because 'environmental stress' differs for each species and for each life-stage. In their review paper, Underwood and Fairweather (1986) suggest that, in testing the generality of 'Environmental Stress Models', there is a requirement for standardised experimental designs in similar habitats across gradients.

My thesis addresses these issues by using different life stages of habitat-forming species from similar environments and standardised experimental methods across wave action gradients at sites within and between hemispheres.

Table 6.1. A summary table of the major null hypotheses tested in each chapter.

Chapter	H_o	Fail to Reject	Reject
2	A) Biomass, species richness and habitat associations are equal across wave exposure gradients.		✓
3	B) Zygote attachment times are equal for algal species from different wave exposures in New Zealand and Oregon.		✓
4	C) Growth and survival of early post-settlement stages of algae across wave exposures are equal.		✓
	D) The effects of invertebrate grazers are equal across exposures.	✓	
	E) The importance of biological and physical factors to early life stages of algae is the same across exposures in Oregon and New Zealand	✓	
5	F) Adult canopy and corallines have no effect on *Durvillaea antarctica* recruitment.		✓
	G) Fish grazing has no effect on *Durvillaea antarctica* recruitment, distribution and abundance.		✓

6.2. Population Ecology Perspective

I did quantitative sampling to compare percent cover, abundance, biomass and species richness of communities from different wave exposures. This was done to generate hypotheses about the processes responsible for observed patterns in communities across exposures. The motivation for this was that while wave exposure is often used as a baseline tests of environmental stress on intertidal community structure, rarely are there contextual community structure data presented. My results indicated that grazer abundance was not significantly different across exposures but did vary across sites within exposures. However, clear patterns were found in the distribution and

biomass of large brown algae across exposures (Table 6.1A), with low shore biomass largely determined by the presence or absence of *Durvillaea antarctica*.

To understand the relative importance of biological and physical processes affecting habitat-forming algae I approached the problem from a population ecology perspective and investigated processes affecting growth and survival at different life-stages (Table 6.1B). I made the assumption that all algae could 'theoretically' arrive at all wave exposures, although recent studies have shown great differences in the dispersal capabilities of algal spores in the nearshore environment that can affect the density of settlement (Reed, 1990a,b; Amsler et al., 1992; Gaylord et al., 2002). I acknowledge that density dependent factors are important but this was not tested in my study (see discussion chapter 3). I then tested the relative abilities of habitat-forming algae in NZ and Oregon to remain attached to an artificial substratum when given different lengths of attachment time. My results indicate that the greater length of time required for secure attachment alone can explain the absence of protected shore species like *Hormosira banksii* and *Cystophora torulosa* from wave exposed situations in New Zealand. In Oregon, I repeated the same experiments using the fucoid algae *Fucus gardneri* and *Pelvetiopsis limitata* that are most abundant at sheltered sites but are constrained to the upper tidal zone in exposed and semi-exposed situations. My results indicate that the low abundance of *F. gardneri* and *P. limitata* in lower tidal zones at exposed sites may be related to the 6 hours these species required to attach securely. Further comparative studies testing the time required for low shore habitat-forming algae to attach securely could elucidate the importance of this factor in determining the community structure of algal communities along intertidal wave exposure gradients.

Once early life stages of algae have attached securely there are myriad factors that affect their growth and survival (Vadas et al. 1992; Hurd, 2000; Reed, 2000; also see chapter 4 discussion). I tested the growth and survival of early life stages of several species of habitat-forming algae in the presence and absence of grazing invertebrates across wave exposure gradients in New Zealand and Oregon (Table 6.1C, D, E). This is

significant because a major goal of marine ecologists has been to determine if similar processes are acting to produce similar patterns of species on intertidal shores world-wide (Stephenson and Stephenson, 1949, 1972; Menge and Farrell, 1989).

Community structure models, like the Environmental Stress Model (Menge and Sutherland, 1987), predict that grazing will me most important in determining community structure at lower levels of environmental stress. A significant result of my study was that the 'importance' of invertebrate grazing to early life stages of algae was great, and did not appear to decline across wave exposures gradients in New Zealand or Oregon. This is in contrast to predictions of the 'Environmental Stress Model' of Menge and Sutherland (1987) (Table 6.1D, E). In most cases the early life stages of these algae were completely removed by invertebrate grazers before they reached the visible recruit stage at c.60 days regardless of exposure (see chapter 4). Another major result of the early life-stage transplant experiments was that in most cases, where grazers were excluded, greatest growth of all algae was recorded at exposed sites regardless of hemisphere (Table 6.1C, E). This is significant because faster growth has important implications for population (Vadas et al. 1992) and community structure (Menge and Farrell, 1989) by reducing the length of time microscopic stages remain vulnerable to grazing effects (Vadas et al, 1992; Underwood, 1991), by decreasing population turnaround time (Connell and Sousa, 1983) and by affecting the relative competitive hierarchies of species (Dayton et al., 1984). A peak in the relative importance of competition to community structure at intermediate levels of environmental stress is predicted by the Menge and Sutherland (1987) 'Environmental Stress Model'. In this respect my results stand in contrast to the predictions of the 'Environmental Stress Model' because if growth is used as a reasonable indicator of physiological stress, these early life stages were clearly not stressed at greater wave exposures. Because growth rates tended to be greatest at the highest exposures for all species, my results infer that competition may therefore be greatest at the highest exposures in the absence of grazers. In my study, the grazing effect was not significantly different across exposures and so one likely effect of increased

growth rates of algae is crowding with potential consequences of density dependent effects in further growth and survival (Schiel, 1981; Ang, 1991a). Therefore, in my model there may be negative feedback mechanisms that appear to mimic results of environmental stress but are actually density dependent effects.

Also highlighted by my experiments was that, within sites of similar exposures, there were significant differences in the importance of factors like sedimentation, grazing and growth of algae. These findings emphasize the difficulties in determining and defining wave exposure in meaningful ways that allow testing of 'Environmental Stress Models'.

Survival of germlings was low, even when caged from grazers, providing further evidence that early-life stages could be a bottle-neck for algal populations (Reed, 1990; Vadas et al. 1992). Many of the exact processes affecting survival rates of these early life stages require further examination (Hurd, 2000). However, there was an interesting interaction between wave action and sedimentation in New Zealand and Oregon. A recent study by Schiel et al. (in review) suggests that sedimentation can have significant effects on the attachment and growth of early life stages of habitat-forming algae and that these effects may explain the inability of the exposed shore species *Durvillaea antarctica* to recruit into more sheltered areas in New Zealand. Continued study into the relative abilities of early life stages of habitat-forming algae to withstand the effects of sedimentation is required. Other areas for further study using early life stages of habitat-forming algae include testing how recruitment is affected by interactions with nutrients, sand, sub-canopy species like coralline algae, the effects of ephemeral algae and their interactions with settlement density and grazing.

The final experimental chapter in this thesis tested hypotheses relating to the processes responsible for the distribution and abundance of *Durvillaea antarctica* across exposures. I did this at two scales. At a fine scale I tested the effects of substratum and canopy on recruitment of *Durvillaea antarctica* (Table 6.1F), the major biomass contributor and habitat-forming alga on exposed shores of southern New Zealand (See

chapter 2). At a broader scale I also transplanted recruit stages of *D. antarctica* across exposures and across coastlines in an attempt to explain its absence from more sheltered situations (Table 6.1G). A key result from both experiments was that *D. antarctica* can recruit directly underneath adult canopies, particularly if coralline algae are removed, although their absence was not always necessary. Recruitment outside canopies was often unsuccessful because of the grazing effects of the butterfish *Odax pullus*. My results indicate that adult canopies of *D. antarctica* may provide recruits with some protection from fish grazing. In most cases *D. antarctica* recruits transplanted outside cages and away from adult canopies were grazed down to the stipe by fish grazing. This finding is important because no other examples of herbivorous fish controlling the distribution and abundance of large intertidal brown algae could be found in the literature (See chapter 5). This has interesting implications for community structure on the west coast of the south island where *D. antarctica* is only found in any abundance on off-shore rocks and steep cliff faces (pers obs., see chapter 2). My results suggest that the grazing effects of the butterfish *O. pullus* are largely responsible for the restricted distribution of *D. antarctica* on this very exposed coastline. Because *D. antarctica* is a major biomass contributor and habitat-former, the factors affecting its distribution could potentially affect community structure and the flow of nearshore nutrients through the intertidal communities on this highly productive coastline (Menge et al., 1999).

6.3. Integration of approaches

Through experimental manipulations I have used habitat-forming algae and their associated communities to test interactions between demographic stages of plants and herbivores across a wave exposure gradient. Consequently, I have used an integrated community ecology and population ecology approach (See general introduction). This is a critical advancement as traditionally, models of community structure have been based on a trophic level interactions (e.g. Hairston et al. 1960; Paine, 1966). More recently, attempts have been made to integrate the effects of recruitment (Menge and

Sutherland, 1987) and nutrient supply (Menge, 1992; van de Koppel et al. 1996) to these models. Community models have been particularly useful for comparing the importance of processes over large scales (eg. Menge and Farrell, 1989; Menge et al. 1999). However, due to the complexity of variables within these models their predictions are often difficult to test experimentally (Menge and Farrell, 1989). Communities in the lower intertidal zones of temperate areas world-wide are generally dominated by kelps and turfing and encrusting coralline algae (Stephenson and Stephenson, 1972; Menge and Farrell, 1989; Foster, 1990; Schiel, 1990). The processes controlling their distribution up the shore have been the subject of extensive research (Chapman and Johnson, 1990; see general introduction) but, in spite of this the processes affecting horizontal distributions of algae are little know (Foster, 1990). My studies suggest that the intertidal communities in the lower tidal zone across wave exposures provide an excellent 'model environment' to test predictions of community models.

The results of my studies suggest that an integration of demographic life stage into models of community structure would increase understanding of the relative importance of factors controlling community structure across gradients in wave exposure (Fig. 6.1). Central to this addition are changes in the relative importance of grazing, physiological stress, inter and intra-specific competition, sedimentation and scour across a gradient of wave action depending on demographic stage. My study did not specifically test the effects of inter and intra-specific competition along this gradient but I have included a subjective assessment of their relative importance to each life stage that I encourage others to modify. Because of the variable nature of intertidal rocky shore habitats I am forced to apply certain assumptions to my community stress models that, at first, appear unrealistic but are necessary in order to enable further experimental testing of the predictions of these models across micro and macro-scales (Underwood and Fairweather, 1986). These assumptions are discussed later but they are: that this model applies to a hard rock surface, that the surface is homogeneous, that the surface is at a uniform slope and aspect across wave exposures, that there is no pre-emptive

occupation of space by competitors, that there are no adult canopies and finally, that high settlement will incur density dependent factors.

My thesis examined three demographic stages: settlement (0-72 hrs), early life-stages (72hrs –visible) and recruits (visible - reproductive). The following model predicts the importance of biological and physical factors in determining low-shore community structure in relation to demographic stage (Fig. 6.1).

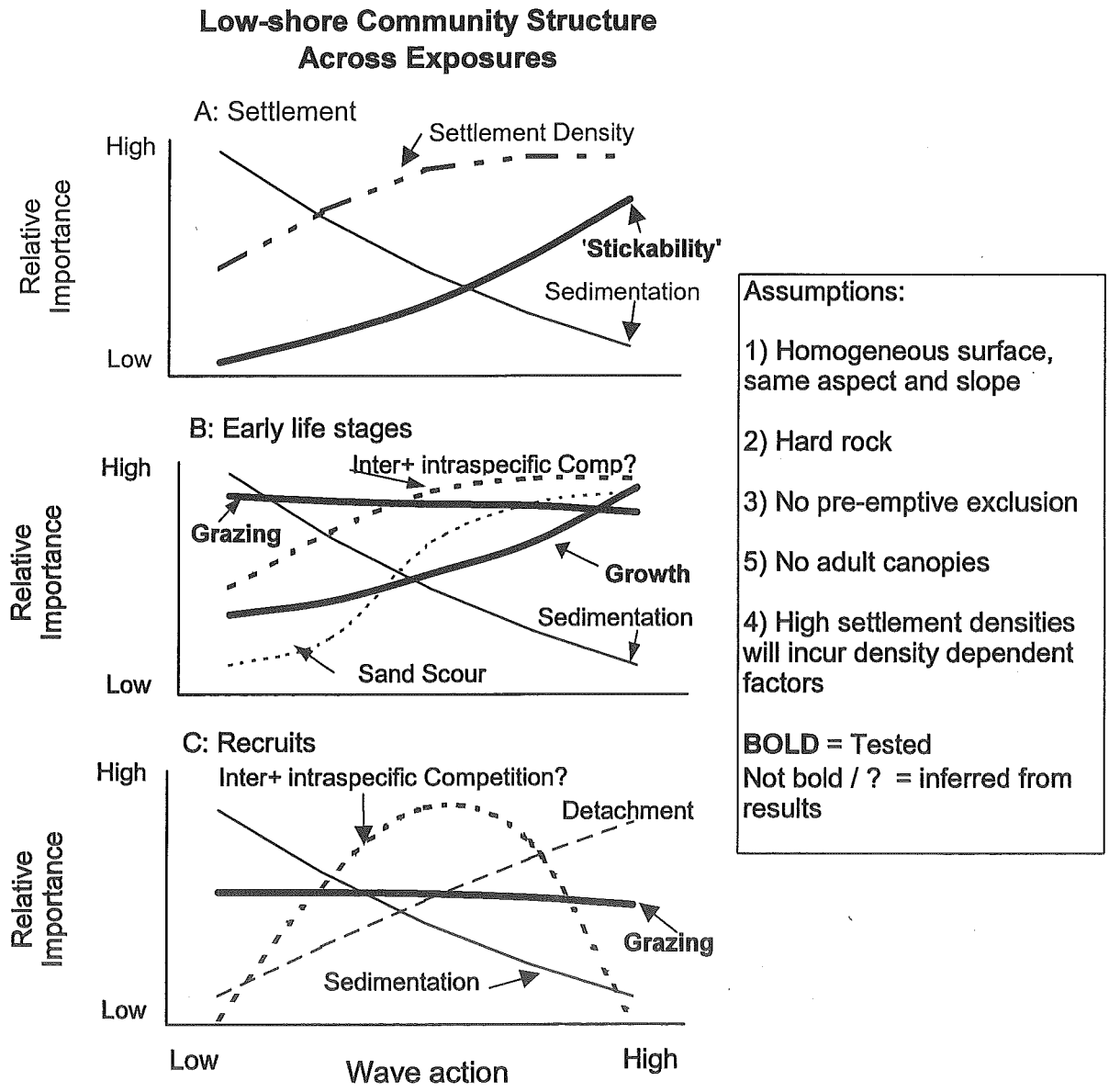

Figure 6.1. Community structure model and its assumptions for demographic stages A) Settlement, B) Early life stage and C) Recruit stage of habitat-forming algae across a wave exposure gradient.

6.4. Model and Predictions

For decades identifying the 'relative importance' of factors determining the structure of communities over intertidal gradients has been a major goal of marine ecologists. However, the term 'relative importance', while frequently used when describing processes is rarely defined and often difficult to test. Menge and Sutherland (1987) refer to 'relative importance' as the proportion of community variance caused by a particular process. Central to this definition a need to understand and illustrate the natural community variance and compare this against the effects of processes tested in standardised experiments in similar habitats at multiple temporal and spatial scales (Underwood and Fairweather, 1986). Menge and Sutherland (1987) suggest that testing the 'relative importance' of processes through experimentation may be so difficult that alternative less precise methods may have to be used. They suggest that the proportion that factors like competition, predation and disturbance contribute to the total number of 'strong links' in interaction-webs be used to identify 'relative importance'. Menge and Sutherland (1987) define a 'strong link' as when one species has an ecologically significant, controlling effect on another and subsequent papers have discussed the relative strengths of direct and indirect interactions in intertidal community structure (Menge et al., 1994; Menge, 1995). However, the ability to test the ecological significance of interactions relies on an understanding of 'relative importance' of process, which leads to a circular problem.

My model approaches this problem from a population ecology perspective and I relate the 'relative importance' of processes to demographic stages of habitat-forming species. This is an important point of difference because the ecological significance of interactions is already incorporated into the model. Habitat-forming species are, by definition, ecologically significant because they provide biomass and habitat.

Settlement

For the settlement stage my study showed that the relative attachment times of algal species can, from the outset, determine their ability to enter and dominate communities across wave exposures (Fig 6.1A). Settlement density depends on numerous factors (Amsler et al., 1992) but in terms of algal community structure in my model settlement density is predicted to be highly important across gradients in wave exposure. Schiel et al. (in review) have shown that sedimentation is inversely related to wave action and that even low levels of sediment can have significant effects on the ability of *Hormosira banksii* and *Durvillaea antarctica* to attach successfully. The model presented here assumes that the substratum is flat and hard and clear of all other organisms because it is recognised that the heterogeneity of the substratum and organisms already occupying the substratum will affect interactions between organisms and determine the ability of species to successfully settle (Amsler et al., 1992; Vadas et al, 1992). My results indicate that under these assumptions community structure can be determined by the relative abilities of the very earliest demographic stages of these key habitat-forming species to attach quickly and securely and overcome the effects of sedimentation across wave exposures.

Early life stages

Early life stages can be a bottleneck for populations of many intertidal organisms (Schiel, 1980; Underwood, 1999; Reed, 2000; see discussion chapter 4). In all early life stage transplant experiments in my study mortality rates were high regardless of wave exposure. Those early life stages that did survive were grazed by invertebrate grazers across all levels of wave exposure (See chapter 4). Therefore, for my community structure model I suggest that grazing by invertebrates is highly important in determining community structure across all levels of wave action. Once again, this depends on the assumptions of the model because it is recognised that surface heterogeneity, slope, aspect, rock type and settlement density can influence the

effectiveness of grazers (Hawkins and Hartnoll, 1983, 1985). Interestingly, growth of all species of algae at this life stage was often greatest at exposed sites (See chapter 4). I use growth as an indicator of physiological stress. Therefore, the model predicts that physiological stress is actually lowest for this life stage at greater wave exposures. In contrast, at more sheltered sites sedimentation is predicted to increase in importance in determining community structure where smothering may occur. Interactions between these variables are important (Vadas et al., 1992) and the effectiveness of grazers may be influenced by the growth rates of algae at wave exposed sites (Cubit, 1984; Kim, 1997) and sedimentation at sheltered sites (Schiel et al., in review). This is indicated in the model by a slight decline in the importance of grazers as wave action increases. The importance of inter and intra-specific competition in determining community structure was not tested but is also predicted to be high across wave exposures for early life stages. My observations suggest that for early life stages competition might be more important at greater wave exposures where growth of habitat-forming algae and ephemeral algae was greatest (see chapter 4 discussion). Another factor inferred in the model was sand scour. The west coast sites in my study, both in Oregon and New Zealand, were often inundated with sand in the low tidal zones and it is predicted that, where present, the interaction between sand, gravel and wave action will be of great importance in determining the survival of early life stages of habitat-forming species and community structure as wave action increases.

Recruit stages

Once intertidal algae reach a size at which they become visible to the human eye they begin to break out of the benthic boundary layer and out of the realm of micro-ecology (Reed, 2000). It is at this demographic stage that much of the study of intertidal populations and communities has occurred (Underwood, 1985). Many species of intertidal algae appear to reach a size, toughness or chemically induced defence refuge from grazing invertebrate herbivores once they reach this stage (see chapter 5).

Consequently, the importance of invertebrate grazing in affecting community structure at this life stage was initially predicted to be low over all levels of wave exposure. However, as shown in chapter 5 the distribution of *Durvillaea antarctica,* a major habitat-forming species on exposed shores around much of New Zealand, appears to be constrained by the grazing effects of the herbivorous fish *Odax pullus.* It is therefore predicted that grazing can be of moderate importance across wave exposure gradients. *D. antarctica* recruits transplanted across exposures became visibly stress at sheltered shores and it is predicted that the importance of physiological stress will increase under more sheltered conditions. While not tested in this study the importance of intra and inter-specific competition are predicted to increase steeply at intermediate levels of wave exposures but decline again as the importance of detachment increases. This subjective assessment is inferred from the implications of the early life-stage model, wherein the combined effects of physiological stress, sedimentation and grazing will reduce the number of species and individual species abundances at very sheltered sites. It is from the recruit life stage that predictions of the Menge and Sutherland (1987) 'Environmental Stress Model' can be integrated. For example, they predict that for basal trophic level species the effects of competition will increase and predation decrease at high recruitment densities.

Summary

A major innovation of this study has been the use of early life stages of habitat-forming algae as model organisms to test ecological theory about the processes determining community structure across wave exposures. This was done across gradients in wave exposure at local, regional and hemispheric scales. My experiments in New Zealand and Oregon highlighted the importance of life history characteristics such as required attachment time and growth rates in early life stage survival. Direct effects of invertebrate grazers were similar across exposures but interactions with sediments and ephemeral algae warrant further study. The distribution of the bull-kelp *Durvillaea*

antarctica outside adult canopies, across exposures and coastlines was largely determined by the grazing effects of the butterfish *Odax pullus* and suggests the importance of fish grazing in structuring low shore algal communities across exposures may have been underestimated.

My experiments show that the relative importance of species specific factors like required attachment time and growth, and general processes like, grazing and wave action can be examined at macro-scales using reciprocal experiments on biologically equivalent species.

Abbott, I. A., Hollenberg, G. J. (1976). Marine Algae of California. Stanford, California, Stanford University Press.

Aberg, P. (1992). A demographic study of two populations of the seaweed *Ascophyllum nodosum*. Ecology 73(4): 1473-1487.

Aberg, P. (1992). Size-based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. Ecology 73(4): 1488-1501.

Aberg, P. (1996). Patterns of reproductive effort in the brown alga *Ascophyllum nodosum*. Marine Ecology Progress Series 138: 199-207.

Adams, N. M. (1994). Seaweeds of New Zealand: An Illustrated Guide. Christchurch, NZ, Canterbury University Press.

Airoldi, L., Cinelli, F. (1997). Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a Mediterranean rocky shore. Journal of Experimental Marine Biology and Ecology 215: 269-288.

Alexander, S. E., Roughgarden, J. (1996). Larval transport and population dynamics of intertidal barnacles: a coupled benthic/oceanic model. Ecological Monographs 66(3): 259-275.

Allen, T. F. H. (1977). Scale in microscopic algal ecology: a neglected dimension. Phycologia 16(3): 253-257.

Amsler, C. D., Neushul, M. (1989). Chemotactic effects of nutrients on spores of the kelps *Macrocystis pyrifera* and *Pterygophora californica*. Marine Biology 102: 557-564.

Amsler, C. D., Reed, D. C., Neushul, M. (1992). The microclimate inhabited by macroalgal propagules. British Phycological Journal 27: 253-270.

Amsler, C. D., Searles, R. B. (1980). Vertical distribution of seaweed spores in a water column offshore of North Carolina. Journal of Phycology 16: 617-619.

Anderson, E. K., North, W. J. (1966). *In situ* studies of spore production and dispersal in the giant kelp, *Macrocystis*. Proc. 5th Int. Seaweed Symp.: 73-86.

Andrew, N. L. (1993). Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in temperate Australia. Ecology 74(2): 292-302.

Andrew, N. L., Jones, G. P. (1990). Patch formation by herbivorous fish in a temperate Australian kelp forest. Oecologia 85(1): 57-68.

Andrew, N. L., Underwood, A. J. (1989). Patterns of abundance of the sea urchin *Centrostephanus rodgersii* (Agassiz) on the central coast of New South Wales, Australia. J. Exp. Mar. Biol. Ecol. 131: 61-80.

Ang(jr), P. O. (1991a). Age- and size- dependent growth and mortality in a population of *Fucus distichus*. Marine Ecology Progress Series 78: 173-187.

Ang(jr), P. O. (1991b). Natural dynamics of a *Fucus distichus* (phaeophyceae, fucales) population: reproduction and recruitment. Marine Ecology Progress Series 78: 71-85.

Ang(jr), P. O., DeWreede, R. E. (1992). Density-dependence in a population of *Fucus distichus*. Marine Ecology Progress Series 90: 169-181.

Bader, C. N. (1998). The ecology of the butterfish *Odax pullus* around the Kaikoura peninsula. Zoology. Christchurch, University of Canterbury: 178pp.

Ballintine, W. J. (1961). A biologically-defined exposure scale for the comparative description of rocky shores. Field Studies 1: 1-19.

Barkai, A., Branch, G. M. (1988). The influence of predation and substratal complexity on recruitment to settlement plates: a test of the theory of alternative states. Journal of Experimental Marine Biology and Ecology 124: 215-237.

Batham, E. J. (1956). Ecology of southern New Zealand sheltered rocky shore. Transactions of the Royal Society of New Zealand 84(2): 447-465.

Batzli, G. O. (1969). Distribution of biomass in rocky intertidal communities on the pacific coast of the United States. Journal of Animal Ecology 38: 531-546.

Becker, K. (1993). Attachment strength and colonization patterns of two macrofouling species on substrata with different surface tension (in situ studies). Marine Biology 117: 301-309.

Begum, M. (1980). The development of the embryo *Hormosira banksii* (Turner) Decaisne (Phaeophyceae, Fucales) in laboratory culture. Unpublished PhD thesis, University of Auckland: 138.

Bell, E. C., Denny, M. W. (1994). Quantifying "wave exposure:" a simple device for recording maximum velocity and results of its used at several field sites. Journal of Experimental Marine Biology and Ecology 181: 9-29.

Bellgrove, A., Clayton, M. N., Quinn, G. P. (1997). Effects of secondarily treated sewage effluent on intertidal macroalgal recruitment processes. Marine Freshwater Research 48: 137-46.

Benedetti-Cecchi, L., Cinelli, F. (1992). Effects of canopy cover, herbivores and substratum type on patterns of *Cystoseira* spp. settlement and recruitment in littoral rockpools. Marine Ecology Progress Series 90: 183-191.

Benedetti-Cecchi, L., Cinelli, F. (1993). Early patterns of algal succession in a midlittoral community of the Mediterranean sea: a multifactorial experiment. Journal of Experimental Marine Biology and Ecology 169: 15-31.

Bergquist, P. L. (1959). A statistical approach to the ecology of *Hormosira banksii*. Botanica Marina 1: 22-53.

Bertness, M. D., Garrity, S. D., Levings, S. C. (1981). Predation pressure and gastropod foraging: a tropical-temperate comparison. Evolution 35(5): 995-1007.

Black, R. (1974). Some biological interactions affecting intertidal populations of the kelp *Egregia laevigata*. Marine Biology 28: 189-198.

Black, R. (1976). The effects of grazing by the limpet, *Acmaea insessa*, on the kelp, *Egregia laevigata*, in the intertidal zone. Ecology 57: 265-277.

Blanchette, C. A. (1996). Seasonal patterns of disturbance influence recruitment of the sea plam, *Postelsia palmaeformis*. Journal of Experimental Marine Biology and Ecology 197: 1-14.

Blanchette, C. A. (1997). Size and survival of intertidal plants in response to wave action: a case study with *Fucus gardneri*. Ecology 78(5): 1563-1578.

Bourget, E., DeGuise, J., Daigle, G. (1994). Scales of substratum heterogeneity, structural complexity, and the early establishment of a marine epibenthic community. Journal of Experimental Marine Biology and Ecology 181: 31-51.

Bourget, E., Lapointe, L., Himmelman, J. H., Cardinal, A. (1994). Influence of physical gradients on the structure of a northern rocky subtidal community. Ecoscience 1(4): 285-299.

Brawley, S. H., Adey, W. H. (1981a). The effect of micrograzers on algal community structure in a coral reef microcosm. Marine Biology 61: 167-177.

Brawley, S. H., Adey, W. H. (1981b). Micrograzers may affect macroalgal density. Nature 292: 177.

Brawley, S. H., Johnson, L. E. (1991). Survival of fucoid embryos in the intertidal zone depends upon developmental stage and microhabitat. Journal of Phycology 27: 179-186.

Brawley, S. H., Johnson, L. E. (1992). Gametogensis, gametes and zygotes: an ecological perspective on sexual reproduction in the algae. British Phycological Journal 27: 233-252.

Brawley, S. H., Johnson, L. E. (1993). Predicting desiccation stress in microscopic organisms: the use of agarose beads to determine evaporation within and between intertidal microhabitats. Journal of Phycology 29: 528-535.

Brawley, S. H., Johnson, L. E., Pearson, G. A., Speransky, V., Li, R., Serrao, E. (1999). Gamete release at low tide in fucoid algae: maladaptive or advantageous. American Zoology 39: 218-229.

Brawley, S. H., Wetherbee, R., Quatrano, R. S. (1976). Fine-structural studies of the gametes and embryo of *Fucus vesiculosus* L. (Phaeophyta) I. Fertilization and pronuclear fusion. Journal of Cell Science 20: 233-254.

Brawley, S. H., Wetherbee, R., Quatrano, R. S. (1976). Fine-structural studies of the gametes and embryo of *Fucus vesiculosus* L. (Phaeophyta) II. The cytoplasm of the egg and young zygote. Journal of Cell Science 20: 255-271.

Brown, M. T. (1987). Effects of desiccation on photosynthesis of intertidal algae from a Southern New Zealand shore. Botanica Marina 30: 121-127.

Bustamante, R. H., Branch, G. M. (1996a). The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. Journal of Experimental Marine Biology and Ecology 196: 1-28.

Bustamante, R. H., Branch, G. M. (1996b). Large scale patterns and trophic structure of southern African rocky shores: the role of geographic variation and wave exposure. Journal of Biogeography 23: 339-351.

Bustamante, R. H., Branch, G. M., Eekhout, S. (1997). The influences of physical factors on the distribution and zonation patterns of South African rocky-shore communities. South African Journal of Marine Science 18: 119-136.

Caffey, H. M. (1985). Spatial and temporal variation in settlement and recruitment of intertidal barnacles. Ecological Monographs 55(3): 313-332.

Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. Annual Review of Ecological Systems 27: 477-500.

Camus, P. (1994). Recruitment of the intertidal kelp *Lessonia nigrescens* Bory in Northern Chile: successional constraints and opportunities. Journal of Experimental Marine Biology and Ecology 184: 171-181.

Carpenter, R. C. (1986). Partitioning herbivory and its effects on coral reefs algal communities. Ecological Monographs 56(4): 345-363.

Carpenter, S. R., Kitchell, J. F., Hodgson, J. R. (1985). Cascading trophic interactions and lake productivity. Bioscience 35: 634-639.

Carrington, E. (1990). Drag and dislodgement of an intertidal macroalga: consequences of morphological variation in *Mastocarpus papillatus* Kutzing. Journal of Experimental Marine Biology and Ecology 139: 185-200.

Catchpole, W. R., Wheeler, C. J. (1992). Estimating plant biomass: a review of techniques. Australian Journal of Ecology 17: 121-131.

Chapman, A. R. O. (1984a). Population and community ecology of seaweeds.

Chapman, A. R. O. (1984b). Reproduction, recruitment and mortality in two species of *Laminaria* in southwest Nova Scotia. Journal of Experimental Marine Biology and Ecology 78: 99-109.

Chapman, A. R. O. (1985). Demography. Handbook of Phycological Methods, Ecological Field methods: Macroalgae. M. Littler and D. S. Littler. Cambridge, Cambridge University Pres.

Chapman, A. R. O. (1986). Age versus stage: an analysis of age- and size- specific mortality and reproduction in a population of *Laminaria longicruris*. Journal of Experimental Marine Biology and Ecology 97: 113-122.

Chapman, A. R. O. (1989). Abundance of *Fucus spiralis* and ephemeral seaweeds in a high eulittoral zone: effects of grazers, canopy and substratum type. Marine Biology 102: 565-572.

Chapman, A. R. O. (1995). Functional ecology of fucoid algae: twenty-three years of progress. Phycologia 34(1): 1-32.

Chapman, A. R. O., Johnson, C. R. (1990). Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. Hydrobiologia 192: 77-121.

Chapman, V. J. (1965). The physiological ecology of some New Zealand seaweeds. Proceedings of the International seaweed symposium 5: 29-54.

Charters, A. C., Neushul, M., Coon, D. (1973). The effect of water motion on algal spore adhesion. Limnology and Oceanography 18(6): 884-896.

Charters, A. C., Neushul, M., Coon, D. A. (1972). Effects of water motion on algal spore attachment. Proc. Int. Seaweed Symp. 7: 243-247.

Chiswell, S. M., Schiel, D. R. (2001). Influence of along-shore advection and upwelling on coastal temperature at Kaikoura Peninsula, New Zealand. New Zealand Journal of Marine and Freshwater Research 33: 307-317.

Choat, J. H., Ayling, A. M. (1987). The relationship between habitat structure and fish faunas on New Zealand reefs. J. Exp. Mar. Biol. Ecol 110: 257-284.

Choat, J. H., Bellwood, D. R. (1985). Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. Marine Biology 89: 221-234.

Choat, J. H., Clements, K. D. (1998). Vertebrate herbivores in marine and terrestrial environments: a nutritional ecology perspective. Annual Review Of Ecology And Systematics 29: 375-403.

Choat, J. H., Clements, K.D. (1992). Diet in odacid and aplodactylid fishes from Australia and New Zealand. Australian Journal of Marine and Freshwater Research. 43(6): 1451-1459.

Choat, J. H., Clements, K.D. (1993). Daily feeding rates in herbivorous labroid fishes. Marine Biology 117(2): 205-211.

Choat, J. H., Schiel, D. R. (1981). Matters Arising - micrograzers may affect macroalgal density. Nature 292: 177.

Choat, J. H., Schiel, D. R. (1982). Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. Journal of Experimental Marine Biology and Ecology 60: 129-162.

Clayton, M. N. (1990). The adaptive significance of life history characters in selected orders of marine brown macroalgae. Australian Journal of Ecology 15: 430-452.

Clayton, M. N. (1992). Propagules of marine macroalgae: structure and development. British Phycological Journal 27: 219-232.

Clements, K. D. (1985). Feeding in two New Zealand herbivorous fish, the butterfish *Odax pullus* and the marble fish, *Aplodactylus arctidens*. Zoology, University of Auckland: 201.

Clements, K. D., Choat, J. H. (1993). Influence of season, ontogeny and tide on the diet of the temperate marine herbivorous fish *Odax pullus* (Odacidae). Marine Biology 117(2): 213-220.

Clements, K. D., Choat, J. H. (1995). Fermentation in tropical marine Herbivorous fishes. Physiological Zoology 68(3): 355-378.

Clements, K. D., Choat, J. H. (1997). Comparison of herbivory in the closely-related marine fish genera Girella and Kyphosus. Marine Biology 127(4): 579-586.

Clements, K. D., Glesson, V.P., Slaytor, M. (1994). Short-chain fatty acid metabolism in temperate marine herbivorous fish. Journal of Comparative Physiology B Biochemical Systemic and Environmental Physiology 164(5): 372-377.

Clements, K. D., Rees, D. (1998). Preservation of inherent contractility in isolated gut segments from herbivorous and carnivorous marine fish. Journal of Comparative Physiology B Biochemical Systemic and Environmental Physiology 168(1): 61-72.

Cole, R. G. (1999). Trophic relationships between fishes and benthic organisms on north-eastern New Zealand reefs. Vie et Milieu 49(4): 201-212.

Connell, J. H. (1961). Effect of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. Ecological Monographs 31: 61-104.

Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42(4): 710-723.

Connell, J. H. (1972). Community interactions on marine rocky intertidal shores. Annual Review of Ecological Systems 3: 169-192.

Connell, J. H. (1974). Field experiments in marine ecology. Experimental marine biology. R. Marsical. New York, Academic Press.

Connell, J. H. (1975). Some mechanisms producing structure in natural communities: A model and evidence from field experiments. Ecology and evolution of communities. M. L. Cody and J. M. Diamond. Cambridge, Massachusetts and London, The Belknap Press and Harvard University Press: 460-499.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. Science 199(1302-1309).

Connell, J. H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. Journal of Experimental Marine Biology and Ecology 93: 11-45.

Connell, J. H., Slayter, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111: 1119-1144.

Connell, J. H., Sousa, W. P. (1983). On the evidence needed to judge ecological stability or persistence. The American Naturalist 121(6): 789-824.

Connolly, S. R., Roughgarden, J. (1998). A latitudinal gradient in northeast pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. The American Naturalist 151(4): 311-325.

Coon, D. A., Neushul, M., Charters, A. C. (1972). The settling behaviour of marine algal spores. Proc. Int. Seaweed Symp. 7: 237-242.

Creed, J. C., Norton, T. A., Kain (Jones), J. M. (1997). Intraspecific competition in *Fucus serratus* germlings: The interaction of light, nutrients and density. Journal of Experimental Marine Biology and Ecology 212: 211-223.

Cubit, J. D. (1984). Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. Ecology 65(6): 1904-1917.

Dalby, D. H., 1985. Exposure grades as a monitoring tool. Rocky Shore Survey and Monitoring Workshop, May 1st to 4th 1984. Hiscock, K., (Ed). pp. 55-58.

Dalby, D. H., Cowell, E. B., Syratt, W. J., Crothers, J. H. (1978). An exposure scale for marine shores in Western Norway. Journal of Marine Biological Association of the UK 58: 975-996.

Davison, I. R., Johnson, L. E., Brawley, S. H. (1993). Sublethal stress in the intertidal zone: Tidal emersion inhibits photosynthesis and retards development in embryos of the brown alga *Pelvetia fastigiata*. Oecologia 96(4): 483-492.

Dayton, P. K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41(4): 351-387.

Dayton, P. K. (1973). Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palaeformis* ruprecht. Ecology 54(2): 433-438.

Dayton, P. K. (1975). Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecological Monographs 45: 137-159.

Dayton, P. K., Currie, V., Gerrodette, T., Keller, B. D., Rosenthal, R., Ven Tresca, D. (1984). Patch dynamics and stability of some Californian kelp communities. Ecological Monographs 54(3): 253-289.

Dayton, P. K., Tegner, M. J. (1984) The importance of scale in community ecology: a kelp forest example with terrestrial analogs. Chapter 17 *in* P. W. Price, C. N. Slobodchikoff, and W.S. Gaud, editors. A new ecology: novel approaches to interactive systems. Wiley, New York, USA.

Dayton, P. K., Tegner, M. J., Parnell, P. E., Edwards, P. B. (1992). Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecological Monographs 62(3): 421-445.

Denley, E. J., Dayton, P. K. (1985). Competition among macroalgae. Handbook of Phycological Methods, Ecological Field Methods: Macroalgae. M. Littler and D. S. Littler. Cambridge, Cambridge University Press.

Denny, M. W. (1985). Water Motion. Handbook of Phycological Methods, Ecological Field Methods: Macroalgae. M. M. Littler and D. S. Littler. Cambridge, Cambridge University Press.

Denny, M. W. (1987a). Life in the maelstrom: the biomechanics of wave-swept rocky shores. Trends in Ecology and Evolution 2(3): 61-66.

Denny, M. W. (1987b). Lift as a mechanism of patch initiation in mussel beds. Journal Of Experimental Marine Biology And Ecology 113(3): 231-245.

Denny, M. W. (1995). Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. Ecological Monographs 65: 371-418.

Denny, M. W., Shibata, M. F. (1989). Consequences of surf-zone turbulence for settlement and external fertilization. The American Naturalist 134(6): 859-889.

Denny, M. W., Brown, V., Carrington, E., Kraemer, G., Miller, A. (1989). Fracture mechanics and the survival of wave-swept macroalgae. Journal of Experimental Marine Biology and Ecology 127: 211-228.

Denny, M. W., Gaines, S. G. (1990). On the prediction of maximum intertidal wave forces. Limnology and Oceanography 55: 1-15.

Denny, M. W., Wethey, D. S. (2001). Physical processes that generate patterns in marine communities. Marine Community Ecology. M. D. Bertness, S. D. Gaines and M. E. Hay. Massachusetts, Sinauer Associates, Inc.: 3-37.

Dethier, M. N. (1981). Heteromorphic algal life histories: the seasonal pattern and responses to herbivory of the brown crust, *Ralfsia californica*. Oceologia 49: 333-339.

Devinny, J. S., Volse, L. A. (1978). Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. Marine Biology 48: 343-348.

Deysher, L., Norton, T. A. (1982). Dispersal and colonization in *Sargassum muticum*. Journal of Experimental Marine Biology and Ecology 56: 179-195.

Deysher, L. E., Dean, T. A. (1986). In situ recruitment of sporophytes of the giant kelp, *Macrocystis pyrifera* (L.) C.A. Agardh: effects of physical factors. Journal of Experimental Marine Biology and Ecology 103: 41-63.

Doblin, M. A., Clayton, M. N. (1995). Effects of secondarily-treated sewage effluent on the early life-history stages of two species of brown macroalgae: Hormosira banksii and Durvillaea potatorum. Marine Biology 122: 689-698.

Dromgoole, F. I. (1980). Dessication resistance of intertidal and subtidal algae. Botanica Marina XXIII: 149-159.

Dudgeon, S. R., Johnson, A. S. (1992). Thick vs thin: thallus morphology and tissue mechanics influence differential drag and dislodgement of two co-dominant seaweeds. Journal of Experimental Marine Biology and Ecology 165: 23-43.

Duggins, D. O., Deither, M. N. (1985). Experimental studies of herbivory and algal competition in a low intertidal habitat. Oceologia 67: 183-191.

Ebeling, A. W., Hixon, M. A. (1991). Tropical and temperate reef fishes: comparison of community structures. Sale, P.F. [Ed.]. The ecology of fishes on coral reefs. Academic Press, Inc., San Diego, New York etc.

Edgar, G. J., Burton, H. R. (2000). The biogeography of shallow-water macrofauna at Heard Island. Papers-and-Proceedings-of-the-Royal-Society-of-Tasmania 133(2): 23-26.

Fairweather, P. G. (1991). Implications of 'supply-side' ecology for environmental assessment and management. Trends In Ecology & Evolution 6(2): 60-63.

Farrell, T. M. (1989). Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. Journal of Experimental Marine Biology and Ecology 128: 57-73.

Farrell, T. M. (1991). Models and mechanisms of succession: an example from a rocky intertidal community. Ecological Monographs 61(1): 95-113.

Fletcher, R. L., Callow, M. E. (1992). The settlement, attachment and establishment of marine algal spores. British Phycological Journal 27: 303-329.

Forbes, M. A., Hallam, N. D. (1978). Gamete structure and fertilization in the brown alga *Hormosira banksii*. British Phycological Journal 13: 299-310.

Forbes, M. A., Hallam, N. D. (1979). Embryogenesis and substratum adhesion in the brown alga *Hormosira banksii*. British Phycological Journal 14: 69-81.

Foster, M. S. (1975). Algal succession in a *Macrocystis pyrifera* forest. Marine Biology 32: 313-329.

Foster, M. S. (1975). Regulation of algal community development in a *Macrocystis pyrifera* forest. Marine Biology 32: 331-342.

Foster, M. S. (1982). Factors controlling the intertidal zonation of *Iridaea Flaccida* (Rhodophyta). J. Phycol. 18: 285-294.

Foster, M. S. (1990). Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. Hydrobiologia 192: 21-33.

Foster, M. S., Schiel, D. R. (1987). Kelp Communities and sea otters: keystone species of just another brick in the wall? Ecological Studies 65: 247.

Foster, M. S., Sousa, W. P. (1985). Succession. Handbook of Phycological Methods, Ecological Field Methods: Macroalgae. M. Littler and D. S. Littler. Cambridge, Cambridge University Press.

Friedland, M. T., Denny, M. W. (1995). Surviving hydrodynamic forces in a wave-swept environment: consequences of morphology in the feather boa kelp, *Egregia menziesii*. Journal of Experimental Marine Biology and Ecology 190: 109-133.

Gaines, S. D., Bertness, a. D. (1992). Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360: 579-580.

Gaines, S. D., Denny, M. W. (1993). The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. Ecology 74(6): 1677-1692.

Gaylord, B. (1999). Detailing agents of physical disturbance: wave-induced velocities and accelerations on a rocky shore. Journal of Marine Biology and Ecology 239: 85-124.

Gaylord, B., Blanchette, C. A., Denny, M. W. (1994). Mechanical consequences of size in wave-swept algae. Ecological Monographs 64(3): 287-313.

Gaylord, B., Reed, D. C., Raimondi, P. T., Washburn, L., McLean, S. R. (2002). A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. Ecology 83(5): 1239-1251.

Geography Department (2002) University of Canterbury, velocity data courtesy of Anna Taylor (Ph.D. student) Geography Department.

Gerard, V. A., Mann, K. H. (1979). Growth and production of *Laminaria longicruris* (phaeophyta) populations exposed to different intensities of water movement. Journal of Phycology 15: 33-41.

Graham, M. H. (1996). Effect of high irradiance on recruitment of the giant kelp *Macrocystis* (Phaeophyta) in shallow water. Journal of Phycology 32: 903-906.

Hairston, N. G., Smith, F. E., Slobodkin, L. B. (1960). Community structure, population control, and competition. Amer. Nat. 94: 421-425.

Hansson, L. A., Johansson, L., Persson, L. (1987). Effects of fish grazing on nutrient release and succession of primary producers. Limnology And Oceanography 32(3): 723-729.

Hardy, F. G., Moss, B. L. (1979). The effects of the substratum on the morphology of the rhizoids of *Fucus* germlings. Estuarine and Coastal Marine Science 9: 577-584.

Harlin, M. M., Lindbergh, J. M. (1977). Selection of substrata by seaweeds: optimal surface relief. Marine Biology 40: 33-40.

Hartog den, C. (1968). The littoral environment of rocky shores as a border between the sea and the land and between the sea and fresh water. Blumea 16: 374-393.

Hawes, I., Smith, R. (1995). Effect of current velocity on the detachment of thalli of *Ulva lactuca* (Chlorophyta) in a New Zealand estuary. Journal of Phycology 31: 875-880.

Hawkins, S. J., Hartnoll, R. G. (1983). Grazing on intertidal algae by marine invertebrates. Oceanogr. Mar. Biol. Annu. Rev 21: 195-282.

Hawkins, S. J., Hartnoll, R. G. (1985). Factors determining the upper limits of intertidal canopy-forming algae. Marine Ecology Progress Series 20: 265-271.

Hay, C. H. (1977). A biological study of *Durvillaea antarctica* (Chamisso) Hariot and *D. willana* Lindauer in New Zealand. Unpublished Ph.D. thesis, Zoology Department, University of Canterbury, Christchurch.

Hay, C. H. (1979a). Nomenclature and taxonomy within the genus *Durvillaea Bory* (Phaeophyceae: Durvilleales Petrov). Phycologia 18(3): 191-202.

Hay, C. H. (1979b). Some factors affecting the upper limit of the southern bull kelp *Durvillaea antarctica* (Chamisso) Hariot on two New Zealand shores. Journal of the Royal Society of New Zealand 9(3): 279-289.

Hay, M. E. (1981). The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology 61(3): 739-750.

Hay, M. E. (1986). Associational plant defences and the maintenance of species diversity: turning competitors into accomplices. American Naturalist 128(5): 617-641.

Hay, M. E. (1991a). Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. Sale, P.F. [Ed.]. The ecology of fishes on coral reefs. Academic Press, Inc., San Diego, New York etc.

Hay, M. E. (1991b). Marine-terrestrial contrasts in the ecology of plant chemical defences against herbivores. Trends In Ecology & Evolution 6(11): 362-365.

Hay, M. E. (1996). Marine chemical ecology: what's known and what's next? Journal Of Experimental Marine Biology And Ecology 200(1-2): 103-134.

Hay, M. E., Duffy, J. E., Fenical, W., Gustafson, K. (1988a). Chemical defence in the seaweed *Dictyopteris delicatula*: differential effects against reef fishes and amphipods. Marine Ecology Progress Series 48(2): 185-192.

Hay, M. E., Duffy, J. E., Paul, V. J., Renaud, P. E., Fenical, W. (1990). Specialist herbivores reduce their susceptibility to predation by feeding on the chemically defended seaweed *Avrainvillea longicaulis.* Limnology And Oceanography 35(8): 1734-1743.

Hay, M. E., Kappel, Q. E., Fenical, W. (1994). Synergisms in plant defences against herbivores: interactions of chemistry, calcification, and plant quality. Ecology 75(6): 1714-1726.

Hay, M. E., Paul, V. J., Lewis, S. M., Gustafson, K., Tucker, J., Trindell, R. N. (1988b). Can tropical seaweeds reduce herbivory by growing at night? Diel patterns of growth, nitrogen content, herbivory and chemical versus morphological defences. Oecologia 75(2): 233-245.

Hickford, M. J. H. (1993). Effects of gill-netting on reef fish populations in central New Zealand. Zoology. Christchurch, University of Canterbury: 287.

Hickford, M. J. H., Schiel, D. R. (1995). Catch vs count: Effects of gill-netting on reef fish populations in southern New Zealand. J. Exp. Mar. Biol. Ecol 188: 215-232.

Hixon, M. A., Brostoff, W. N. (1981). Fish grazing and community structure of Hawaiian reef algae. Proc. Int. Coral Reef Symp. No 2: 507-514.

Hixon, M. A., Brostoff, W. N. (1983). Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. Science 220: 511-513.

Hixon, M. A., Brostoff, W. N. (1985). Substrate characteristics, fish grazing, and epibenthic reef assemblages off Hawaii. Bulletin Of Marine Science 37(1): 200-213.

Hixon, M. A., Brostoff, W. N. (1996). Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. Ecological Monographs 66(1): 67-90.

Hoffmann, A. J. (1987). The arrival of seaweed propagules at the shore: a review. Botanica Marina 30: 151-165.

Hoffmann, A. J., Camus, P. (1989). Sinking rates and viability of spores from benthic algae in central Chile. Journal of Experimental Marine Biology and Ecology 126: 281-291.

Hoffmann, A. J., Santelices, B. (1991). Banks of algal microscopic forms: hypotheses on their functioning and comparisons with seed banks. Marine Ecology Progress Series 79: 185-194.

Hoffmann, A. J., Ugarte, R. (1985). The arrival of propagules of marine macroalgae in the intertidal zone. Journal of Experimental Marine Biology and Ecology 92: 83-95.

Horn, M. H., Murray, S. N., Edwards, T. W. (1982). Dietary selectivity in the field and food preferences in the laboratory for two herbivorous fishes (*Cebidichthys violaceus* and *Xiphister mucosus*) from a temperate intertidal zone. Marine Biology 67: 237-246.

Horn, M. H., Neighbors, M. A., Murray, S. N. (1986). Herbivore responses to a seasonally fluctuating food supply: growth potential of two temperate intertidal fishes based on the protein and energy assimilated from their macroalgal diets*. J. Exp. Mar. Biol. Ecol 103: 217-234.

Horn, P. L. (1984). Beachrock erosion due to feeding by *Chiton (Sypharochiton) pelliserpentis* at mudstone bay, Kaikoura, New Zealand. Mauri Ora 11: 57-61.

Huang, R., Boney, A. D. (1983). Effects of diatom mucilage on the growth and morphology of marine algae. J. Exp. Mar. Biol. Ecol. 67: 79-89.

Hunter, M. D., Price, P. W. (1992). Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73(3): 724-732.

Hurd, C. L. (2000). Water motion, marine macroalgal physiology, and production. J. Phycol. 36(3): 453-472.

Hurd, C. L., Dring, M. J. (1990). Phosphate uptake by intertidal algae in relation to zonation and season. Marine Biology 107: 281-289.

Hurd, C. L., Dring, M. J. (1991). Desiccation and phosphate uptake by intertidal fucoid algae in relation to zonation. British Phycological Journal 26: 327-333.

Hurd, C. L., Galvin, R. S., Norton, T. A., Dring, M. J. (1993). Production of hyaline hairs by intertidal species of Fucus (Fucales) and their role in phosphate uptake. Journal Of Phycology 29(2): 160-165.

Hurd, C. L., Harrison, P. J., Druehl, L. D. (1996). Effect of seawater velocity on inorganic nitrogen uptake by morphologically distinct forms of *Macrocystis integrifolia* from wave-sheltered and exposed sites. Marine Biology 126(2): 205-214.

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54(2): 187-211.

Jenkins, S. R., Hawkins, S. J., Norton, T. A. (1999). Interaction between a fucoid canopy and limpet grazing in structuring a low shore intertidal community. Journal of Experimental Marine Biology and Ecology 233(1): 41-63.

Jernakoff, P. (19851). An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. Journal of Experimental Marine Biology and Ecology 88: 287-302.

Jernakoff, P. (1985b). Interactions between the limpet *Patelloida latistrigata* and algae on an intertidal rock platform. Marine Ecology Progress Series 23: 71-78.

Johnson, C. R., Mann, K. H. (1986). The crustose coralline alga, *Phymatolithon foslie*, inhibits the overgrowth of seaweeds without relying on herbivores. Journal of Experimental Marine Biology and Ecology 96: 127-146.

Johnson, M. P., Burrows, M. T., Hartnoll, R. G., Hawkins, S. J. (1997). Spatial structure on moderately exposed rocky shores: patchy scales and the interactions between limpets and algae. Marine Ecology Progress Series 160: 209-215.

Jones, G. P., Andrew, N. L. (1990). Herbivory and patch dynamics on rocky reefs in temperate Australasia: The roles of fish and sea urchins. Australian Journal of Ecology 15: 505-520.

Jones, W. E., Demetropoulos, A. (1968). Exposure to wave action: measurement of an important ecological parameter on rocky shores on Anglesey. Journal of Experimental Marine Biology and Ecology 2: 46-63.

Kautsky, L., Kautsky, H. (1989). Algal species diversity and dominance along gradients of stress and disturbance in marine environments. Vegetation 83: 259-267.

Kendrick, G. A., Walker, D. I. (1991). Dispersal distances for propagules of *Sargassum spinuligerum* (Sargassaceae, Phaeophyta) measured directly by vatial staining and venturi suction sampling. Marine Ecology Progress Series 79: 133-138.

Kendrick, G. A., Walker, D. I. (1994). Role of recruitment in structuring beds of *Sargassum* spp. (Phaephyta) at Rottnest Island, Western Australia. Journal of Phycology 30: 200-208.

Kennelly, S. J. (1987). Inhibition of kelp recruitment by turfing algae and consequences for an Australian kelp community. Journal of Experimental Marine Biology and Ecology 112: 49-60.

Keough, M. J. (1983). Patterns of recruitment of sessile invertebrates in two subtidal habitats. Journal of Experimental Marine Biology and Ecology 66: 213-245.

Keough, M. J., & Quinn, G. P. (1991). Causality and the choice of measurements for detecting human impacts in marine environments. Australian Journal of Marine and Freshwater Research 42: 539-554.

Keough, M. J., Quinn, G. P. (1998). Effects of periodic disturbances from trampling on rocky intertidal algal beds. Ecological Applications 8(1): 141-161.

Kevekordes, K., Clayton, M. N. (2000). Development of Hormosira banksii (Phaeophyceae) embryos in selected components of secondarily-treated sewage effluent. Journal of Phycology 36(1): 25-32.

Kilar, J. A., McLachlan, J. (1989). Effects of wave exposure on the community structure of a plant-dominated, fringing-reef platform: intermediate disturbance and disturbance-mediated competition. Marine Ecology Progress Series 54: 265-276.

Kim, J. H. (1997). The role of herbivory, and direct and indirect interactions, in algal succession. Journal of Experimental Marine Biology and Ecology 217: 119-135.

Kim, J. H., DeWreede, R. E. (1996). Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. Marine Ecology Progress Series 133: 217-228.

Knox, G. A. (1953). The intertidal ecology of Taylor's Mistake, Banks Peninsula. Transactions of the Royal Society of New Zealand. 81(2): 189-220.

Koehl, M. A. R. (1984). How do benthic organisms withstand moving water? American Zoology 24: 57-70.

Koehl, M. A. R., Alberte, R. S. (1988). Flow, flapping, and photosynthesis of *Nereocystis luetkeana*: a functional comparison of undulate and flat blade morphologies. Marine Biology 99: 435-444.

Larned, S. T., Atkinson, M. J. (1997). Effects of water velocity on NH_4 and PO_4 uptake and nutrient-limited growth in the macroalga *Dictyosphaeria cavernosa.* Marine Ecology Progress Series 157: 295-302.

Leigh, E. G., Paine, R. T., Quinn, J. F., Suchanek, T. H. (1987). Wave energy and intertidal productivity. Proceedings of the National Academy of Sciences USA 84: 1314-1318.

Lewis, J. R. (1964). The ecology of rocky shores. London, English Universities Press.

Lewis, S. M. (1986). The role of herbivorous fishes in the organization of a Caribbean reef community. Ecological Monographs 56(3): 183-200.

Lewis, S. M., Wainwright, P. C. (1985). Herbivore abundance and grazing intensity on a Caribbean coral reef. Journal of Experimental Marine Biology and Ecology 87: 215-228.

Liu, J. H. (1993). The effects of physical factors and grazing by limpets on the colonization, growth and composition of intertidal algae on a rocky shore at Cape D'Aguilar, Hong Kong. Asian Marine Biology 10: 27-40.

Lohse, D. P. (1993). The effects of substratum type on the population dynamics of three common intertidal animals. Journal of Experimental Marine Biology and Ecology 173: 133-154.

Lohse, D. P. (1993). The importance of secondary substratum in a rocky intertidal community. Journal of Experimental Marine Biology and Ecology 166: 1-17.

Lotze, H. K., Worm, B. (2000). Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. Marine Ecology Progress Series 200(14): 167-175.

Lotze, H. K., Worm, B., Sommer, U. (2000). Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. Oikos 89(1): 46-58.

Lotze, H. K., Worm, B., Sommer, U. (2001). Strong bottom-up and top-down control of early life stages of macroalgae. Limnology and Oceanography 46(4): 749-757.

Lubchenco, J. (1978). Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. The American Naturalist 112(983): 23-39.

Lubchenco, J. (1980). Algal zonation in the New England rocky intertidal community: an experimental analysis. Ecology 61(2): 333-344.

Lubchenco, J. (1983). *Littorina* and *Fucus*: effects of herbivores substratum heterogeneity, and plant escapes during succession. Ecology 65(4): 1116-1123.

Lubchenco, J., Cubit, J. (1980). Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. Ecology 61(3): 676-687.

Lubchenco, J., Menge, B. A. (1978). Community development and persistence in a low rocky intertidal zone. Ecological Monographs 48: 67-94.

Luning, K., Neushul, M. (1978). Light and temperature demands for growth ad reproduction of Laminarian gametophytes in southern and central California. Marine Biology 45: 297-309.

Madsen, J. D., Chambers, P. A., James, W. F., Koch, E. W., Westlake, D. F. (2001). The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia 444: 71-84.

Marsden, I. D. (1985). Between the tides on the Kaikoura Peninsula. Mauri Ora 12: 69-93.

Mathieson, A. C., Guo, Z. (1992). Patterns of fucoid reproductive biomass allocation. British Phycological Journal 27: 271-292.

McCook, L. J., Chapman, A. R. O. (1997). Patterns and variations in natural succession following massive ice-scour of a rocky intertidal seashore. Journal of Experimental Marine Biology and Ecology 214(1-2): 121-147.

McLachlan, J. (1974). Effects of temperature and light on growth and development of embryos of *Fucus edentatus* and *F. distichus* ssp. *distichus*. Can. J. Bot. 52: 943-951.

McLay, C. L. (1995). Keys to the marine invertebrates of the Kaikoura peninsula: A laboratory manual. E. P. F. S. Kaikoura New Zealand, Zoology Department, University of Canterbury.

McQuaid, C. D., Branch, G. M. (1984). Influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. Marine Ecology Progress Series 19: 145-151.

McQuaid, C. D., Branch, G. M. (1985). Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. Marine Ecology Progress Series 22: 153-161.

Meekan, M. G. (1986). The distribution and abundance of the herbivorous fish *Odax pullus* and its influence on the food plant *Ecklonia radiatai* within a temperate reef environment. Zoology, University of Auckland: 68.

Meekan, M. G., Choat, J. H. (1997). Latitudinal variation in abundance of herbivorous fishes: A comparison of temperate and tropical reefs. Marine Biology 128(3): 373-383.

Melville, A. J., Connell, S. D. (2001). Experimental effects of kelp canopies on subtidal coralline algae. Australian Ecology 26(1): 102-108.

Menge, B. A. (1976). Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs 46: 355-393.

Menge, B. A., (1978a). Predation intensity on a rocky intertidal community. Relation between predator foraging activity and environmental harshness. Oecologia 34, 1-16.

Menge, B. A., (1978b). Predation intensity on a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. Oecologia 34, 17-35.

Menge, B. A. (1983). Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia 58: 141-155.

Menge, B. A. (1992). Community regulation: under what conditions are bottom-up factors important on rocky shores? Ecology 73(3): 755-765.

Menge, B. A. (1995). Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs 65(1): 21-74.

Menge, B. A., Berlow, E. L., Blanchette, C. A., Navarrete, S. A., Yamada, S. B. (1994). The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs 64(3): 249-286.

Menge, B. A., Branch, G. M. (2001). Rocky intertidal communities. Marine Community Ecology. M. D. Bertness, S. D. Gaines and M. Hay. Sunderland, Sinauer Associates: 221-251.

Menge, B. A., Daley, B. A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P. M., Hudson, G., Burnaford, J. L. (1999). Top-down and bottom-up regulation of New Zealand rocky intertidal communities. Ecological Monographs 69(3): 297-330.

Menge, B. A., Daley, B. A., Wheeler, P. A., Dahlhoff, E., Sanford, E., Strub, P. T. (1997). Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences 94: 14530-14535.

Menge, B. A., Farrell, T. M. (1989). Community structure and interaction webs in shallow marine hard-bottom communities: Tests of an environmental stress model. Adv. Ecol. Res 19: 189-262.

Menge, B. A., Farrell, T. M., Olson, A. M., Tamelen, P. v., Turner, T. (1993). Algal recruitment and the maintenance of a plant mosaic in the low intertidal region on the Oregon coast. Journal of Experimental Marine Biology and Ecology 170: 91-116.

Menge, B. A., Olson, A. M. (1990). Role of scale and environmental factors in regulation of community structure. TREE 5(2): 52-57.

Menge, B. A., Sutherland, J. P. (1976). Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. The American Naturalist 110(973): 351-369.

Menge, B. A., Sutherland, J. P. (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. The American Naturalist 130(5): 730-757.

Moore, L. B. (1961). Distribution patterns in New Zealand seaweeds. Totara 9: 18-23.

Moorjani, S., Jones, W. F. (1972). Spore attachment and development in some coralline alga. Br. Phycol. J. 7: 282.

Morton, J., Miller, M. (1968) The New Zealand Sea Shore. London, Auckland, Collins 653p.

Moss, B. (1975). Attachment of zygotes and germlings of *Ascophyllum nodosum* (L.) Le Jol. (Phaeophyceae, Fucales). Phycologia 14(2): 75-80.

Naylor, M. (1953). The New Zealand species of *Durvillaea**. Transactions of the Royal Society of New Zealand 80: 277-297.

Nelson, W. A. (1994). Distribution of macroalgae in New Zealand: An archipelago in space and time. Botanica Marina 37: 221-233.

Neushul, M. (1967). Studies of subtidal marine vegetation in western Washington. Ecology 48(1): 83-94.

Neushul, M., Coon, D. A., Charters, A. C. (1972). Direct observation of algal spores under natural conditions. Proc. Int. Seaweed Symp. 7: 231-247.

Norton, T. A. (1983). The resistance to dislodgement of *Sargassum muticum* germlings under defined hydrodynamic conditions. J. mar. biol. Ass. U.K. 63: 181-193.

Norton, T. A. (1991). Conflicting constraints on the form of intertidal algae. British Phycological Journal 26: 203-218.

Norton, T. A. (1992). Dispersal by macroalgae. British Phycological Journal 27: 293-301.

Norton, T. A., Fetter, R. (1981). The settlement of *Sargassum muticum* propagules in stationary and flowing water. Journal of Marine Biological Association of UK 61: 929-940.

Ojeda, F. P., Munoz, A. A. (1999). Feeding selectivity of the herbivorous fish Scartichthys viridis: Effects on macroalgal community structure in a temperate rocky intertidal coastal zone. Marine Ecology Progress Series 28(184): 219-229.

Olson, A. M., Lubchenco, J. (1990). Competition in seaweeds: linking plant traits to competitive outcomes. Journal of Phycology 26: 1-6.

Ortega, S. (1986). Fish predation on gastropods on the pacific coast of Costa Rica. J. Exp. Mar. Biol. Ecol 97: 181-191.

Osborn, J. E. M. (1948). The structure and life history of *Hormosira banksii*. Transactions of the Royal Society of New Zealand 77(1): 47-71.

Osman, R. W., Whitlatch, R. B. (1995). The influence of resident adults on recruitment: a comparison to settlement. Journal of Experimental Marine Biology and Ecology 190: 169-198.

Paine, R. T. (1966). Food Web Complexity and species diversity. The American Naturalist 100(910): 65-75.

Paine, R. T. (1971). A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52: 1096-1106.

Paine, R. T. (1974). Intertidal community structure. Oceologia 15: 93-120.

Paine, R. T. (1979). Disaster, catastrophe, and local persistence of the sea palm *Postelsia palmaeformis*. Science 205: 685-686.

Paine, R. T. (1980). Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49: 667-685.

Paine, R. T. (1984). Ecological determinism in the competition for space. Ecology 65(5): 1339-1348.

Paine, R. T., Levin, S. A. (1981). Intertidal landscape: disturbance and the dynamics of pattern. Ecological Monographs 51(2): 145-178.

Paine, R. T., Castilla, J. C., Cancino, J., (1985). The perturbation and recovery patterns of starfish dominated intertidal assemblages in Chile, New Zealand and Washington State. Am. Naturalist 125, 679-691.

Paul, V. J., Hay, M. E., Duffy, J. E., Fenical, W., Gastafson, K. (1987). Chemical defence in the seaweed Ochtodes secundiramea (Montagne) Howe (Rhodophyta): effects of its monoterpenoid components upon diverse coral-reef herbivores. Journal Of Experimental Marine Biology And Ecology 114(2-3): 249-260.

Pearson, G. A., Brawley, S. H. (1996). Reproductive ecology of *Fucus distichus* (Phaeophyceae): and intertidal alga with successful external fertilization. Marine Ecology Progress Series 143: 211-223.

Pearson, G. A., Brawley, S. H. (1998). A model for signal transduction during gamete release in the fucoid alga *Pelvetia compressa*. Plant Physiology 118: 305-313.

Pearson, G. A., Serrao, E. A., Brawley, S. H. (1998). Control of gamete release in fucoid algae: sensing hydrodynamic condition via carbon acquisition. Ecology 79(5): 1725-1739.

Petraitis, P. S. (1987). Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. Journal of Experimental Marine Biology and Ecology 109: 117-136.

Petraitis, P. S. (1990). Direct and indirect effects of predation, herbivory and surface rugosity on mussel recruitment. Oceologia 83: 405-413.

Petraitis, P. S., Latham, R. E., Niesebaum, R. A., (1989). The maintenance of species diversity by disturbance. Q. Rev. Bio. 64, 393-418.

Pirker, J. G. (1992). Growth, shell-ring deposition, and mortality of paua (*Haliotis iris* Martyn) in the Kaikoura region. Zoology. Christchurch, University of Canterbury: 166.

Polis, G. A. (1994). Food webs, trophic cascades and community structure. Australian Journal of Ecology 19: 121-136.

Pollock, E. G. (1969). Interzonal transplantation of embryos and mature plants of *Fucus*. Proc. Int. Seaweed Symp. 6: 345-356.

Pollock, E. G. (1970). Fertilization in *Fucus**. Planta 92: 85-99.

Povey, A., Keough, M. J., (1991). Effects of trampling on plant and animal populations on rocky shores. OIKOS 61: 355-368.

Powell, A. W. B. (1979). New Zealand Mollusca. Auckland, Collins.

Provasoli, L. (1963). Growing marine seaweeds. Proc. Int. Seaweed Symp. 4: 9-17.

Quatrano, R. S. (1980). gamete release, fertilisation and embryogenesis in the Fucales. Handbook of Phycological Methods, Developmental and Cytological Methods. E. Gantt. Cambridge, Cambridge University Press.

Raffaelli, D. (1979). The grazer-algae interaction in the intertidal zone on New Zealand rocky shores. Journal of Experimental Marine Biology and Ecology 38: 81-100.

Raffaelli, D., Hawkins, S. (1996). Intertidal Ecology. London, Chapman & Hall.

Raimondi, P. T. (1988). Rock type affects settlement, recruitment, and zonation of the barnacle *Chthamalus anispoma* pilsbury. Journal of Experimental Marine Biology and Ecology 123: 253-267.

Raimondi, P. T. (1990). Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. Ecological Monographs 60(3): 283-309.

Reed, D. C. (1987). Factors affecting the production of sporophylls in the giant kelp *Macrocystis pyrifera*. Journal of Experimental Marine Biology and Ecology 113: 61-69.

Reed, D. C. (1990)a. The effects of variable settlement and early competition on patterns of kelp recruitment. Ecology 71(2): 776-787.

Reed, D. C. (1990)b. An experimental evaluation of density dependence in a subtidal algal population. Ecology 71(6): 2286-2296.

Reed, D. (2000). Microecology of macroalgal blooms. J. Phycol. 36(1): 1-2.

Reed, D. C., Amsler, C. D., Ebeling, A. W. (1992). Dispersal in kelps: factors affecting spore swimming and competency. Ecology 73(5): 1577-1585.

Reed, D. C., Anderson, T. W., Ebeling, A. W., Anghera, M. (1997). The role of reproductive synchrony in the colonization potential of kelp. Ecology 78(8): 2443-2457.

Reed, D. C., Foster, M. S. (1984). The effects of canopy shading on algal recruitment and growth in a giant kelp forest. Ecology 65(3): 937-948.

Reed, D. C., Laur, D. R., Ebeling, A. W. (1988). Variation in algal dispersal and recruitment: the importance of episodic events. Ecological Monographs 58(4): 321-335.

Reed, D. C., Neushul, M., Ebeling, A. W. (1991). Role of settlement density on gametophyte growth and reproduction in the kelps *Pterogophora californica* and *Macrocystis pyrifera* (Phaeophyceae). Journal of Phycology 27: 361-366.

Reed, D. C., Raimond, P. T., Carr, M. H., Goldwasser, L. (2000). The role of dispersal and distrubance in determining spatial heterogeneity in sedentary organisms. Ecology 81(7): 2011-2026.

Ricketts, E. F., Clavin, J., Hedgpath, J. W. (1969). Between Pacific tides. Stanford, California, USA, Stanford University Press.

Robles, C. (1982). Disturbance and predation in an assemblage of herbivorous diptera and algae on rocky shores. Oceologia 54: 23-31.

Robles, C. D., Cubit, J. (1981). Influence of biotic factors in an upper intertidal community: dipteran larvae grazing on algae. Ecology 62(6): 1536-1547.

Russel, B. C. (1983). The food and feeding habits of rocky reef fish of north-eastern New Zealand. New Zealand Journal of Marine and Freshwater Research 17: 121-145.

Sala, E. (1997). The role of fishes in the organization of a Mediterranean sublittoral community: II. Epifaunal communities. Journal of Experimental Marine Biology and Ecology 212(1): 45-60.

Sala, E., Boudouresque, C. F. (1997). The role of fishes in the organization of a Mediterranean sublittoral community. I: Algal communities. Journal of Experimental Marine Biology and Ecology 212(1): 25-44.

Sammarco, P. W. (1983). Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure*. Marine Ecology Progress Series 13: 1-14.

Sanders, H. L. (1968). Marine benthic diversity: A comparative study. Amer. Nat. 102: 243-282.

Santelices, B. (1990a). Patterns of organizations of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile. Hydrobiologia 192: 35-57.

Santelices, B. (1990b). Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanogr. Mar. Biol. Annu. Rev 28: 177-276.

Santelices, B. (1996). Seaweed research and utilization in Chile: moving into a new phase. Hydrobiologia 326/327: 1-14.

Santelices, B., Aedo, D. (1999). Evaluating substances that facilitate algal spore adhesion. Hydrobiologia 398/399: 241-246.

Santelices, B., Bobadilla, M. (1996). Gastropod pedal mucus retains seaweed propagules. Journal of Experimental Marine Biology and Ecology 197: 251-261.

Santelices, B., Castilla, J. C., Cancino, J., Schmiede, P. (1980). Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in Central Chile. Marine Biology 59: 119-132.

Santelices, B., Ojeda, F. P. (1984). Recruitment, growth and survival of *Lessonia nigrescens* (Phaeophyta) at various tidal levels in exposed habitats of central Chile. Marine Ecology Progress Series 19: 73-82.

Santelices, B., Paya, I. (1989). Digestion survival of algae: some ecological comparisons between free spores and propagules in faecal pellets. Journal of Phycology 25: 693-699.

Santos, R., Duarte, P. (1996). Fecundity, spore recruitment and size in *Gelidium sesquipedale* (Gelidiales, Rhodophyta). Hydrobiologia 326/327: 223-228.

Schiel, D. R. (1981). A demographic and experimental evaluation of plant and herbivore interactions in subtidal algal stands. Department of Zoology, University of Auckland.

Schiel, D. R. (1988). Algal interactions on shallow subtidal reefs in Northern New Zealand: a review. NZ Journal of Marine and Freshwater Research 22: 481-489.

Schiel, D. R. (1990). Macroalgal assemblages in New Zealand: structure, interactions and demography. Hydrobiologia 192: 59-76.

Schiel, D. R., Andrew, N. L., Foster, M. S. (1995). The structure of subtidal algal and invertebrate assemblages at the Chatham Islands, New Zealand. Marine Biology 123(2): 355-367.

Schiel, D. R., Choat, J. H. (1981). Micrograzers may affect macroalgal density. Nature 292: 177.

Schiel, D. R., Taylor, D. I. (1999). Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand. Journal of Experimental Marine Biology and Ecology 235: 213-235.

Schonbeck, M., Norton, T. A. (1978). Factors controlling the upper limits of fucoid algae on the shore. Journal of Experimental Marine Biology and Ecology 31: 303-313.

Schonbeck, M., Norton, T. A. (1979). An investigation of drought avoidance in intertidal fucoid algae. Botanica Marina XXII: 133-144.

Schonbeck, M. W., Norton, T. A. (1980). Factors controlling the lower limits of fucoid algae on the shore. Journal of Experimental Marine Biology and Ecology 43: 131-150.

Seed, R., (1996). Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. J. Mar. Biol. Assoc. 76, 203-210.

Serrao, E., Brawley, S. H., Hedman, J., Kautsky, L., Samuelsson, G. (1999a). Reproductive success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. Journal of Phycology 35: 254-269.

Serrao, E. A., Alice, L. A., Brawley, S. H. (1999b). Evolution of the Fucaceae (Phaeophyceae) inferred from nrDNA-ITS. Journal of Phycology 35(2): 382-394.

Serrao, E. A., Pearson, G. A., Kautsky, L., Brawley, S. H. (1996). Successful external fertilization in turbulent environments. Proceedings of the National Academy of Sciences *USA* 93: 5286-5290.

Sjotun, K., Fredriksen, S., Rueness, J. (1998). Effect of canopy biomass and wave exposure on growth in *Laminaria hyperborea* (Laminariaceae: Phaeophyta). Eur. J. Phycol. 33: 337-343.

Smith, C. (1992). Diversity in intertidal habitats: an assessment of the marine algae of select high islands in the Hawaiian archipelago. Pacific Science 46(4): 466-479.

Sousa, W. P. (1979). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60(6): 1225-1239.

Sousa, W. P. (1979). Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs 49(3): 227-254.

Sousa, W. P. (1984). Intertidal mosaics: Patch size, propagule availability and spatially variable patterns of succession. Ecology 65(6): 1918-1935.

Sousa, W. P. (2001). Natural disturbance and the dynamics of marine benthic communities. Marine Ecological Communities. M. D. Bertness, S. D. Gaines and M. E. Hay. Sunderland, Massachusetts, Sinauer Associates, Inc.: 85-130.

Sousa, W. P., Schroeter, S. C., Gaines, S. D. (1981). Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. Oecologia 48: 297-307.

South, G. R., Adams, N. M. (1976). The marine algae of the Kaikoura coast - a list of species, National Museum of New Zealand.

South, G. R., Hay, C. H. (1979). Influence of wave action and latitude on morphology and standing crop of New Zealand *Durvillaea antarctica* (Chamisso) Hariot (Phaeophyta, Durvilleales). Journal of the Royal Society of New Zealand 9(3): 289-296.

Spencer, T. (1992). Bioerosion and biomorphology. Oxford, Clarendon Press.

Steinburg, P. D. (1985). Feeding preferences of *Tegula funebralis* and chemical defences of marine brown algae. Ecological Monographs 55(3): 333-349.

Stephenson, T. A., Stephenson, A. (1949). The universal feature of zonation between the tide-marks on rocky coasts. J. Ecol. 36: 289-305.

Stephenson, T. A., Stephenson, A. (1972). Life between the tidemarks on rocky shores. San Francisco, Freeman & Co.

Stevens, C. L., Hurd, C. L. (1997). Boundary-layers around bladed aquatic macrophytes. Hydrobiologia 346: 119-128.

Suchanek, T. H. (1978). The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. Journal of Experimental Marine Biology and Ecology 31: 105-120.

Taylor, D. I., Schiel, D. R. (In Press) Wave-related mortality in zygotes of habitat-forming algae from different exposures in southern New Zealand: the importance of 'stickability', Journal of Experimental Marine Biology and Ecology.

Taylor, P., Littler, M. (1982). The roles of compensatory mortality, physical disturbance, and substratum retention in the development and organization of a sand-influenced, rocky-intertidal community. Ecology 63(1): 135-146.

Thompson, R. C., Wilson, B. J., Tobin, M. L., Hill, A. S., Hawkins, S. J. (1996). Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. Journal of Experimental Marine Biology and Ecology 202: 73-84.

Trowbridge, C. D., Menge, B. A., Lubchenco, J., (1996). Landscape biodiversity patterns on rocky intertidal shores. In: Woodin, S.A., Allen, D.M., Stancyk, S.E., Williams-Howze, J., Feller, R.J., Wethey, D.S., Pentcheff, N.D., Chandler, G.T., Decho, A.W., Coull, B.C., (Eds.), Twenty-fourth Annual Benthic Ecology Meeting, Columbia, South Carolina. 81 pp.

Underwood, A. J. (1978). An experimental evaluation of competition between 3 species of intertidal prosobranch gastropods. Oecologia 33: 185-202.

Underwood, A. J. (1979). The ecology of intertidal gastropods. Adv. Mar. Biol. 16: 111-210.

Underwood, A. J. (1980). The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. Oceologia 46: 201-213.

Underwood, A. J. (1985). Physical factors and biological interactions: the necessity and nature of ecological experiments. The Ecology of Rocky Coasts. P. G. Moore, Seed, R.,. London, Sydney, Auckland, Toronto, Hodder and Staunton: 372-390.

Underwood, A. J. (1986). What is a community? Life Sciences Research Report No 36: 351-367.

Underwood, A. J. (1991). The logic of ecological experiments: a case history from studies of the distribution of macro-algae on rocky intertidal shores. J. mar. biol. Ass. U.K. 71: 841-866.

Underwood, A. J. (1997). Experiments in Ecology; Their Logical Design and Interpretation Using Analysis of Variance. Cambridge, Cambridge University Press: 504 pp.

Underwood, A. J. (1998). Grazing and disturbance: an experimental analysis of patchiness in recovery from a severe storm by the intertidal alga *Hormosira banksii* on rocky shores in New South Wales. Journal of Experimental Marine Biology and Ecology 231: 291-306.

Underwood, A. J. (1999). Physical disturbances and their direct effect on an indirect effect: Responses of an intertidal assemblage to a severe storm. Journal of Experimental Marine Biology and Ecology 232(1): 125-140.

Underwood, A. J. (2000). Experimental ecology of rocky intertidal habitats: What are we learning? Journal of Experimental Marine Biology and Ecology. [print] 250(1-2): 51-76.

Underwood, A. J., Chapman, M. G. (1996). Scales of spatial patterns of distribution of intertidal invertebrates. Oceologia 107: 212-224.

Underwood, A. J., Chapman, M. G., Connell, S. D. (2000). Observations in ecology: You can't make progress on processes without understanding the patterns. Journal of Experimental Marine Biology and Ecology. 250(1-2): 97-115.

Underwood, A. J., Denley, E. J. (1984). Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. Ecological communities, conceptual issues and the evidence. D. R. Strong, D.

Simberloff, L. G. Abele and A. B. Thistle, Princeton University Press: 151-180.

Underwood, A. J., Fairweather, P. G. (1986). Intertidal communities: do they have different ecologies or different ecologists? Proc. Ecol. Soc. Aust. 14: 7-16.

Underwood, A. J., Fairweather, P. G. (1989). Supply-side ecology and benthic marine assemblages. Tree 4(1): 16-20.

Underwood, A. J., Jernakoff, P. (1981). Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oceologia 48: 221-233.

Underwood, A. J., Jernakoff, P. (1984). The effects of tidal height, wave exposure, seasonality and rock pools on grazing and the distribution of intertidal macroalgae in new south wales. Journal of Experimental Marine Biology and Ecology 75: 71-96.

Underwood, A. J., Kingsford, M. J., Andrew, N. L. (1991). Patterns in shallow subtidal marine assemblages along the coast of New South Wales. Australian Journal of Ecology 6: 231-249.

Underwood, A. J., Petraitis, P. S. (1993). Structure of intertidal assemblages in different locations: how can local processes be compared? Chicago and London, The University of Chicago Press.

Vadas, R. L. (1985). Herbivory. Handbook of Phycological Methods, Ecological Field Methods: Macroalgae. M. Littler and D. S. Littler. Cambridge, Cambridge University Press.

Vadas, R. L., Wright, W. A., Miller, S. L. (1990). Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. Marine Ecology Progress Series 61: 263-272.

Vadas, S. R. L., Johnson, S., Norton, T. A. (1992). Recruitment and mortality of early post-settlement stages of benthic algae. British Phycological Journal 27: 331-351.

Valiela, I. (1995). Marine Ecological Processes. New York, Springer-Verlag.

Van Alstyne, K. L., Pelletreau, K., N. (2000). Effects of nutrient enrichment on growth and phlorotannin production in Fucus gardneri embryos. Marine Ecology Progress Series 206: 33-43.

van de Koppel, J., Huisman, J., van der Wal, R., Olff, H. (1996). Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. Ecology 77(3): 736-745.

Vincent W. F., Howard-Williams C., 1991. Distribution and biological properties of oceanic water masses around the South Island, New Zealand. New Zealand J. Mar. Freshwat. Res. 25, 21-42.

Vogel, S. (1981). Life in Moving Fluids. Princeton, Princeton University Press.

Vogel, S. (1984). Drag and flexibility in sessile organisms. American Zoology 24: 37-44.

Vreeland, V., Grotkopp, E., Espinosa, S., Quiroz, D., Laetsch, W. M., West, J. (1993). The pattern of cell wall adhesive formation by *Fucus zygotes*. Hydrobiologia 260/261: 485-491.

Walters, L. J., Wethey, D. S. (1996). Settlement and early post-settlement survival of sessile marine invertebrates on topographically complex surfaces: the importance of refuge dimensions and adult morphology. Marine Ecology Progress Series 137(1-3): 161-171.

Wheeler, W. N. (1980). Effect of boundary layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. Marine Biology 56: 103-110.

Worm, B., Chapman, A. R. O. (1996). Interference competition among two intertidal seaweeds: *Chondrus crispus* strongly affects survival of *Fucus evanescens* recruits. Marine Ecology Progress Series 145: 297-301.

Worm, B., Chapman, A. R. O. (1998). Relative effects of elevated grazing pressure and competition from a red algal turf on two post-settlement stages of *Fucus evanescens*. Journal of Experimental Marine Biology and Ecology 220: 247-268.

Wright, P. J., Reed, R. H. (1990). Effects of osmotic stress on gamete size, rhizoid initiation and germling growth in fucoid algae. British Phycological Journal 25: 149-155.

Wuff, F. V., Field, J. G. (1983). Importance of different trophic pathways in a nearshore benthic community under upwelling and downwelling conditions. Marine Ecology Progress Series 12: 217-228.

Zacharias, M. A., Morris, M. C., Howes, D. E. (1999). Large scale characterisation of intertidal communities using a predictive model. Journal of Experimental Marine Biology and Ecology 239: 223-242.

Appendix A. Summary of sampling results from Chapter 2: Species encountered and identified from sampling across all exposures, sites and tidal heights. The exposures where each species was encountered are sheltered (SH), semi-protected (SP), exposed (EX) and very exposed (VE).

Grouping	Species	Exposure			
		SH	SP	EX	VE
A: Algae					
	Large Brown seaweeds				
	Durvillaea antarctica (Chamisso) Hariot	X		X	
	Hormosira banksii (Turner) Descainse	X	X	X	
	Cystophora retroflexa (Labillardiere) J. Agardh	X	X		
	Cystophora torulosa (R. Brown) J. Agardh	X	X		
	Cystophora scalris (J. Agardh)	X	X		
	Cystophora distentia (J. Agardh)		X		
	Carpophyllum maschalocarpum (Turner) Greville		X	X	
	Xiphophora gladiata (Labillardiere) Montagne		X	X	
	Brown seaweeds				
	Colpomenia peregrina (Sauvageau) Hamel	X	X		
	Adenocystis utricularis (Bory) Skottsberg	X	X		
	Leathesia intermedia Chapman	X	X	X	
	Leathesia difformis (Linnaeus) Areschoug	X	X		
	Herpodiscus durvilleae (Lindauer) South		X	X	
	Halopteris virgata (Hook. F. et Harvey) Adams		X	X	
	Dictoyota dichotoma (Hudson) Lamouroux		X		
	Cladostephus spongiosus (Hudson) C. Agardh		X		
	Glossophora kunthii (C. Agardh) J. Agardh		X		
	Scytothamnus australis (J. Agardh) Hook. f. et Harvey			X	
	Tinocladia novae-zelandiae Kylin		X		
	Ectocarpus siliculosus (Dillwyn) Lyngbye	X	X	X	
	Notheia anomala (Bailey et Harvey)	X	X	X	
	Foliose Red Seaweeds				
	Pleonosporium hirtum (Hook. f. et Harvey) Laing		X	X	
	Anotrichium crinitum (Kuetzing) Baldock		X		
	Ballia callitricha (C. Agardh) Kuetzing		X	X	
	Ballia hirsuta (Wollaston)		X	X	
	Cladhymenia oblongifolia Harvey		X	X	
	Polysiphonia rudis Hook. F. et Harvey		X	X	
	Polysiphonia decipiens Montagne	X	X	X	
	Polysiphonia pernacola Adams	X	X	X	
	Champia novae-zealandia (Hook.f. et Harvey)		X	X	
	Echinothamnion lyallii (Hook f. et Harvey) Kylin			X	
	Bachelotia antillarum (Grunow) Gerloff		X	X	

Callophyllis calliblepharoides (J. Agardh)		X	X	
Griffithsia antarctica (Hook.f. et Harvey)		X	X	
Gracilaria secundata (Harvey)		X	X	
Nothogenia fastigiata (Bory) Parkinson		X	X	
Curdiea flabellata (Chapman)		X	X	
Bryocladia ericoides (Harvey) Schmitz		X	X	
Helminthocladia dotyi (Wormersley)		X	X	
Gigartina decipiens (Hook. F. et. Harvey)		X	X	X
Gigartina livida (Turner) J. Agardh		X	X	X
Gigartina macrocarpa (J. Agardh)		X	X	
Gigartina clavifera (J. Agardh)		X	X	X
Gigartina circumcincta (J. Agardh)			X	X
Gigartina lanceata (J. Agardh)			X	X
Gigartina sp. "Lindauer Exsicc. No. 164"		X	X	
Hymenocladia sanguinea (Harvey) Sparling		X	X	
Gelidium pusillum (Stackhouse) le Jolis		X		
Gelidium caulacantheum (J. Agardh)		X	X	
Laurencia thyrsifera J. Agardh		X	X	
Porphyra columbina (Montagne)		X	X	X
Porphyra sp.(in Nelson 1994: 126)		X	X	X
Stictosiphonia arbuscula (Harvey) King et Puttock		X	X	
Stictosipohnia hookeri (Harvey) Hook. f. et Harvey			X	
Green Seaweeds				
Ulva lactuca Linnaeus	X	X	X	
Enteromorpha bulbosa (Suhr) Montagne	X	X	X	
Enteromorpha linza (Linnaeus) J. Agardh			X	
Chaetomorpha coliformis (Montagne) Kuetzing		X	X	
Caulerpa brownii (C. Agardh) Endlicher		X		
Codium convolutum (Dellow) Silva	X	X		
Codium dimorphum Svedelius			X	
B: Geniculate corallines				
Corallina officinalis (Linnaeus)	X	X	X	X
Jania micrarthrodia (Lamouroux)	X	X		
Haliptilon roseum (Lamarck) Garbary et Johansen		X	X	X
Arthrocardia corymbosa (Lamarck) Decaisne			X	X
Non-geniculate corallines				
Lithothamnion sp.	X	X	X	X
C: Tar species				
Ralfsia verrucosa (Areschoug) J. Agardh	X	X	X	X
Hildenbrandia kerguelensis (Askenasy) Chamberlain		X	X	
Hildenbrandia dawsonii (Ardre) Hollenberg			X	X

D: Filter-feeders				
Mussels				
Mytilus edulis galloprovincialis (Lamarck)	X		X	X
Perna canaliculus (Gmelin)	X		X	X
Xenostrobus pulex (Lamarck)			X	X
Aulacomya ater maoriana (Iredale)	X		X	X
Barnacles				
Epopella plicata (Gray)	X		X	X
Chaemosipho brunnea Moore	X	X	X	X
Chaemosipho columna (Spengler)	X	X	X	X
Tubeworms				
Pomatoceros carinifereus (Gray)	X		X	
Galeolaria hystrix (Moerch)	X		X	
Other bivalves				
Crassotrea gigas (Thunberg)	X			
Protothaca crassicosta (Deshayes)			X	
Modiolarca impacta (Hermann)	X			
E: Predators				
Seastars				
Patiriella regularis (Verrill)	X		X	
Stichaster australis (Verrill)	X		X	X
Astrostole scabra (Hutton)	X		X	
Whelks				
Haustrum haustorium (Gmelin)	X		X	X
Thais orbita (Gmelin)	X		X	X
Cominella maculosa (Martyn)	X	X		
Cominella glandiformis (Reeve)	X	X		
Lepsiella scobina scobina (Quoy & Gaimard)	X	X	X	
Penion sulcatus (Lamarck)	X	X		
Buccinulum lineum lineum (Martyn)	X			
Anemones				
Anthoplura minima		X	X	
Anthoplura rosea			X	
Cricophorus nutrix	X	X		
Isactinia tenebrosa	X	X		
Intertidal insects				
Desis marina (Forster)			X	
Errant Polychaetes				
Perinereis nuntia (Grube)	X	X	X	
Perinereis amblyodonta (Schmarda)	X	X		
Perinereis novaehollandiae				X
Platynereis australis (Schmarda)			X	X
Podarke augustifrons			X	

Eunice rubella (Knox)	X	X		
Eulalia microphylla (Schmarda)	X	X	X	
F: Grazers				
Topshells				
Turbo smaragdus (Gmelin)	X	X	X	
Melagraphia aethiops (Gmelin)	X	X	X	X
Diloma zelandica (Quoy & Gaimard)		X	X	
Diloma nigerrima (Gmelin)		X	X	
Diloma arida (Finlay)		X	X	
Micrelenchus sanguineus (Gray)		X	X	
Maurea punctulata (Martyn)		X	X	
Littorina cincta (Quoy & Gaimard)	X	X	X	X
Littorina unifasciata antipodum Philippi	X	X	X	X
Zeacumantus subcarinatus (Sowerby)			X	X
Zeacumantus lutulentus (Kiener)		X	X	
Risellopsis varia (Hutton)	X	X	X	
Limpets				
Siphonaria australis (Suter)		X		
Siphonaria zealandica (Quoy & Gaimard)	X	X	X	
Benhamina obliquata (Sowerby)		X	X	
Notoacmea scopulina (Oliver)			X	X
Notoacmea parviconoidea (Suter)		X	X	
Notoacmea pileopsis (Quoy & Gaimard)			X	X
Notoacmea helmsi (E.A. Smith)			X	X
Patelloida corticata (Hutton)		X	X	X
Cellana radians (Gmelin)	X	X	X	X
Cellana stellifera (Gmelin)		X	X	X
Cellana denticulata (Gmelin)	X	X	X	X
Cellana ornata (Dillwyn)	X	X	X	X
Chitons				
Ischnochiton maorianus (Iredale)		X	X	
Eudoxochiton nobilis (Gray)			X	
Maorichiton caelatus (Reeve)		X	X	X
Frembleya egregia (Adams)		X	X	
Amaurochiton glaucus (Gray)		X	X	
Onithochiton neglectus (Rochebrune)			X	X
Chiton pelliserpentis (Quoy & Gaimard)	X	X	X	X
Acanthochitona zelandica (Quoy & Gaimard)			X	X
Cryptoconchus porosus (Burrow)		X		
Onchidella nigricans (Quoy & Gaimard)			X	
G: Other invertebrate species				

Isopods				
Pseudodidothea richardsoni			X	
Seriolis latifrons	X	X	X	
Cymodoce australis	X	X	X	
Amphipods				
Family Caprellidae (1species)	X	X		
Family Ingolfiellidae (1species)	X	X		
Family Gammaridae (4 species)	X	X	X	
Family Lysianassidae (1 species)		X		
Platyhelminthes				
Leptoplana sp.	X		X	X
Nematodas				
Pseudocella sp.		X		
Nemertea				
Lineus sp.	X		X	X
Ostracods				
Myodocopa sp.		X	X	
Hydrozoa				
Amphisbetia bispinosa			X	
Polyzoa				
1 Species			X	
Bryozoa				
2 Species			X	
Ascidians				
Pyura pachdermatina			X	
Astericarpa coerulea	X		X	
Cnemidocarpa bicornuata	X		X	
Brittlestars				
Amphipholis squamata (Delle Chiaje)			X	
Crabs				
Petrolisthes novaezelandiae (Filhol)	X	X	X	X
Petrolisthes elongatus (H. Milne Edwards)	X		X	X
Helicarcinus innominatus (Richardson)		X		
Halicarcinus cookii (Filhol)		X	X	
Helice crassa (Dana)		X	X	
Pagurus novizealandiae (Dana)	X	X		
Pagurus traversi (Filhol)		X		